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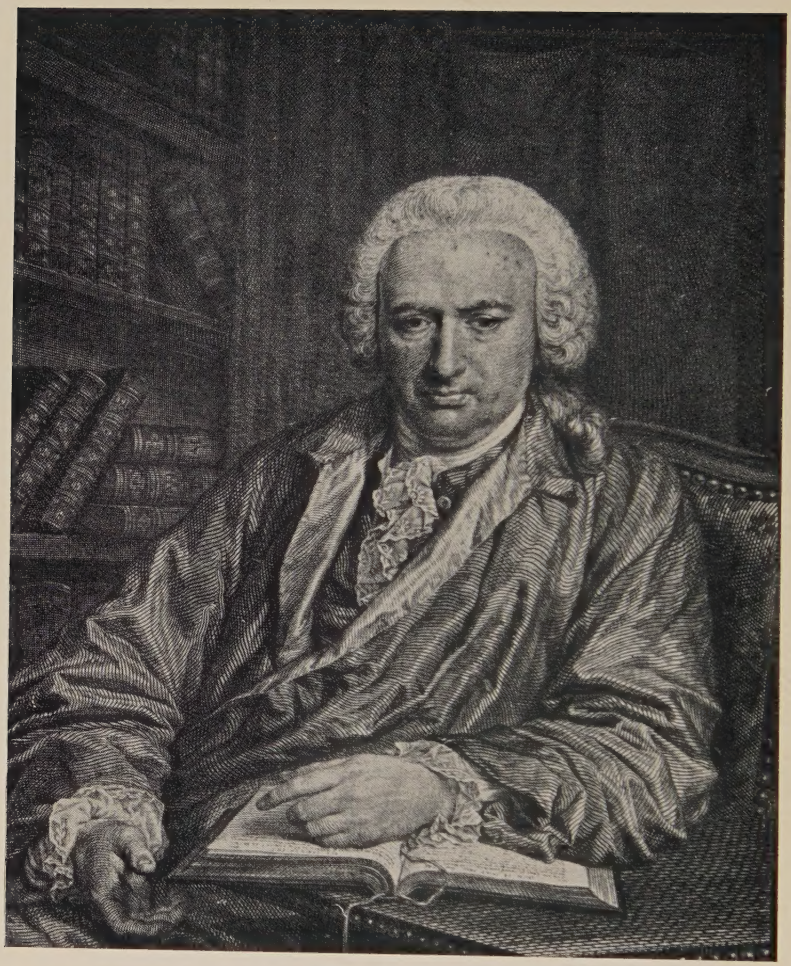

CHARLES BONNET

EARLY THEORIES OF SEXUAL GENERATION

By

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'*We must not surmise or invent,*
but discover, *what Nature does,*
as Bacon very well says.'
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PREFACE

THIS essay is one of the many relaxations from the ties of a more exacting work on the History of Zoology on which I have been engaged for very many years. Probably no one who has worked on a comprehensive treatise of this character has been able to resist the appeal of the numerous backwaters into which from time to time he is inveigled. I have already been turned from the purpose of the parent work on two occasions in order to trace the development of the Anatomical Museum and the history of Anatomical Injections. The present diversion has disclosed many critical points which it is hoped will be of interest to the historian and bibliographer. I have attempted to place the *complete* story of the Preformation Doctrine before the reader, and to avoid the common mistake of ignoring all but the more salient features. If, therefore, parts of the narrative are devoid of arresting incident, it is because the genius of the time was often unenterprising and imitative. All historians of Science soon realize how curiously easy it is to fall into error. I have discovered too many serious lapses in the work of my contemporaries to be guilty of the folly of supposing that my own is free from them. I must therefore rely on the sympathetic understanding of the instructed reader, and expect the inevitable corrections.

My friend Mr. Clifford Dobell, F.R.S., who has made a very careful study of Leeuwenhoek, has been kind enough to contribute to the work a translation of Leeuwenhoek's historic letter on the discovery of the spermatozoa. The manuscript of this letter has not survived, and Mr. Dobell's translation is based on the Dutch and two Latin versions which were printed at the time. He has also revised the translation of the difficult letter by 'Dalenpatius', in the

preparation of which I had the assistance of Dr. W. H. Semple. Mr. A. Hastings White, of the Royal Society, has always cheerfully responded to my almost daily requests for books and advice in various bibliographical entanglements, and my valued colleague, Dr. N. B. Eales, has given material help in revising and preparing the manuscript for the press. The photographic illustrations are the work of Mr. F. C. Padley. Finally I owe grateful acknowledgements to the Research Board of Reading University for a grant in aid of publication.

F. J. C.

Reading
July, 1930.

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I

EARLY HISTORY OF THE SPERMATOZOA[1]

THE discovery of the spermatozoa is one of the major events in the history of Zoology. 'There is', says Leuckart, 'scarcely any discovery in the realm of animal Biology which has aroused so general an interest as the discovery of these motile seminal corpuscles.' Around this real, but almost inscrutable nucleus, are grouped all modern systems of generation, and compared with it they are as evanescent as steam. Rarely in the history of Science have issues of great philosophical and practical importance depended on so circumscribed a foundation, and rarely has any foundation been called upon to support such excessive and shifting loads. The superstructure in fact is constantly undergoing demolition and repair, but the germ endures as the unchanging material basis of it all. The popular fallacy that small things are of necessity contemptible, exemplified by the complacent opinion of Malebranche that 'men were not made to contemplate midges', is sufficiently refuted by the history of the spermatozoa, and we may now proceed to trace that history in some detail.

Before the spermatozoa were actually observed the speculations of Paracelsus that generation is initiated in putrefactions, and may be made the subject of an alchemical experiment, had aroused expectations of spectacular discoveries. Man, he says, may be generated without a natural father or mother, and to do this

'let the sperm of a man by itself be putrefied in a gourd glass, sealed up, with the highest degree of putrefaction in horse-dung, for the space of forty days, or so long until it begin to be alive, move, and stir, which may easily be seen. After this time it will be something like a man, yet transparent, and without a body. Now after this, if

[1] In these two chapters the history of the spermatozoa is traced only in so far as it has any connexion, real or supposed, with observation. The relation of the spermatozoa to the preformation doctrine, which is a philosophical conception having no observational basis, is dealt with elsewhere.

it be every day warily, and prudently nourished and fed with the arcanum of man's blood, and be for the space of forty weeks kept in a constant, equal heat of horse-dung, it will become a true, and living infant, having all the members of an infant, which is born of a woman, but it will be far less. This we call *Homunculus* or artificial man. . . . Now this is one of the greatest secrets, that God ever made known to mortal, sinful man.' [1]

The word Homunculus occurs in Cicero, and was used by Paracelsus to indicate a man made artificially, in which sense it was employed by a number of later writers, some of whom refer to the 'Homunculus of Paracelsus'. The Homunculus of Sterne in *Tristram Shandy* savours more of Paracelsus than of Leeuwenhoek, or perhaps, as is more likely, Sterne is using the term in its original literary sense as meaning simply a little man. Paracelsus disliked women, which may explain his attempt to produce a foetus without the co-operation of a mother.

The occurrence of fertilizing particles in the male semen was assumed by Gardinius in 1623, but it is to Christiaan Huygens in 1678 that we owe the first *published* description of the spermatozoa. After mentioning animals which arise in corruptions, he says that

'there is another kind which must have a different origin. Such for example are those which one discovers with the microscope in the semen of animals, which seem to belong to it, and are present in such great quantity as to compose almost the whole of it. They are formed of a transparent substance, their movements are very brisk, and their shape is similar to that of frogs before their limbs are formed. This discovery, *which was made in Holland* for the first time, seems very important, and should give employment to those interested in the generation of animals.'

No names are mentioned in this note, which was published on August 15th, but in a letter dated March 26th, 1678, Huygens admits having seen Leeuwenhoek's letter of November 1677 [2] (published in 1679), and he also knew of

[1] Sir Thomas Browne commenting on this says, 'I am not of Paracelsus' mind, that boldly delivers a receipt to make a man without conjunction'.

[2] This was probably shown him by his father, Constantin Huygens, to whom Leeuwenhoek had sent a copy of this letter.

Leeuwenhoek's letter of December 3rd of the same year. Huygens returns to the spermatozoa in a letter to Grew dated June 6th, 1678, in which he mentions that he had of late devoted his attention to improving microscopes, being prompted thereto by the discovery of the animalcules in the semen of animals by Hammius, a student of Leyden, which animals, he says, he has often seen. In a communication to the French Academy dated July 30th, 1678, Huygens describes small animals like tadpoles which he had found in the semen of the dog. Finally in his 'Opuscula Posthuma' he says that the 'most wonderful and extraordinary of microscopic sights is the animals in the male semen. They appear as an immense swarm of little fishes having the form of frog's tadpoles before they have acquired their feet'. On this evidence it is manifest that, although Huygens does not mention Leeuwenhoek by name in his published notes, his own work is nothing more than a verification of a discovery communicated to him by Leeuwenhoek.

On August 29th, 1678, a further communication on the spermatozoa was published under the name of Hartsoeker. At that time Hartsoeker was not able to write in French, and the note, as he admitted later, was drafted by Huygens. In it he mentions very briefly the semen of the cock as containing animals *like little eels*, which therefore differed from the tadpole-like animalcules found in the semen of other types. Hartsoeker was of course quite right in this, and it must be admitted that he was the first to see the spermatozoa of a bird. There is no claim to priority in this note, but the letters of Hartsoeker published recently disclose the source of his information on the spermatozoa. In letters to Huygens dated March 14th and 25th, 1678, that is before the date of Huygens' first letter, Hartsoeker describes his method of making microscope lenses. He fuses in a lamp flame single beads of glass, which are thereafter neither ground nor polished. When observing, the microscope is directed against the bright blue sky, in order to obtain a brilliant background. In the first of these letters, he gives a figure of the spermatozoa showing the head and tail, but it is small

and crude, nor does it exhibit any internal structure. He does not state from what animal it was derived. In the second letter he says that the more he examines the seminal animalcules, the more difficult it is to describe their form exactly. They have, he thinks, a projecting muzzle, a flat back, round belly, and a tail ten or twelve times the length of the body. The human animalcules are said to agree with those of the dog, except that in the dog they are a little more oblong. He announces that he is about to examine the semen of the horse and bull. Another crude figure is given which also shows no internal structure. One remark in this letter is important. He accuses Leeuwenhoek (quite wrongly) of finding vessels in the seminal animalcules, and in his next letter he is anxious to know what Leeuwenhoek made of the seminal animalcules in the rabbit, but as Leeuwenhoek's first published letter on the spermatozoa did not appear until 1679, it follows that Hartsoeker is in the same position as Huygens, and must have obtained his first knowledge of the spermatozoa from Leeuwenhoek, either directly, or indirectly through Huygens. In a further letter dated April 4th, 1678, he claims to have seen the seminal animalcules of the bull, but was not able to observe them properly, and he mentions that they occur also in the cock and drake. In man he believes that they can change the shape of their bodies, which explains why it is difficult to determine their structure. It should be noted that, up to this point, Hartsoeker gives no hint or suggestion of the existence of a complex structure in the seminal animalcule.

In 1694 Hartsoeker makes his first claim to the discovery of the spermatozoa. He states that it is more than twenty years since he examined the semen of animals with microscopes, and discovered, and published for the first time, that it was crowded with an infinity of animals like the tadpoles of the frog. In man and quadrupeds the animals were of the tadpole type, but in birds they were worm-like. This discovery, he says, he communicated to Malebranche. In 1674, when the alleged discovery was made, Hartsoeker would be but eighteen years of age, and, further, he forgets that his

note was published in 1678 and not in 1674. Many years later, after Leeuwenhoek was dead, Hartsoeker revived his claim to the discovery of the spermatozoa in an elaborate and scornful attack on Leeuwenhoek, but he himself died before it was published. We may at the outset reasonably ask why he nursed his grievances for over forty years, and only reduced them to writing when his opponent was unable to reply.

Hartsoeker, in this interesting but mendacious document, informs us that he visited Leeuwenhoek at his house three times—in 1672–3 (with his father), 1679, and 1697–8. On his second visit he incurred the enmity of Leeuwenhoek by a contemptuous criticism of his work and methods amounting almost to an accusation of bad faith. The difference between the two men at that time, both in respect of age and reputation, was considerable, and it is therefore not surprising than when Hartsoeker begged for information as to Leeuwenhoek's methods, he was told that they were communicated only to his wife and daughter, after which the great man excused himself, and the youthful critic was curtly dismissed. At his third visit Hartsoeker was accompanied by the Burgomaster of Delft, who was requested not to disclose his companion's identity, which, after an interval of almost twenty years, might be regarded as impenetrable. Nevertheless he did so, whereupon Leeuwenhoek received Hartsoeker with an air of disdain, his eyes flashed with indignation and contempt, and he roughly turned him out of the house, without attempting to show him anything.

Hartsoeker, having explained how and why he had learnt nothing from Leeuwenhoek, proceeds to criticize Leeuwenhoek's letter No. 113, dated December 17th, 1698. He asserts that Leeuwenhoek, prior to this letter, had never made known that the discovery of the seminal animalcules had been communicated to him by Ham. On the contrary Leeuwenhoek had insinuated that the discovery was his own, and had allowed himself to be acclaimed as the discoverer, without attempting to undeceive the world. When, however, he had read the passage in his (Hartsoeker's) *Dioptrique*

of 1694, he abandoned his own pretensions to the discovery, and resuscitated a student of medicine named Ham, to whom he attributed it. From these statements we can only conclude that Hartsoeker had either forgotten, or had never seen, Leeuwenhoek's letter dated 1677, which was published in the *Philosophical Transactions* for 1679, in which he quite definitely attributes the discovery of the spermatozoa to Ham. Further, Hartsoeker's three private letters to Huygens written in 1678, bearing dates anterior to his published description of the spermatozoa of the same year, establish the fact that he was already acquainted with Leeuwenhoek's work on the spermatozoa at the very time that he is repudiating any knowledge of it.

In the letter No. 113, to which Hartsoeker refers, Leeuwenhoek mentions that many years before an elderly man with his son [young Hartsoeker] had been to see him. He is surprised that Hartsoeker should claim as his own a discovery which belongs properly to Ham, who by his modesty, good sense and diligence was well qualified to discover the secrets of Nature. What, asks Leeuwenhoek, must Hartsoeker have been like twenty-five years ago, that is in 1674? But, replies Hartsoeker, he was born in 1656, and would then be eighteen years of age, his eyes would be as good as those of a man of forty [Leeuwenhoek would be forty-two in 1674], he had perfect lenses which Nature made for him [the fused beads of glass], and sufficient curiosity to wish to examine everything which came under his notice, in which occupation, as witness Leeuwenhoek himself, he lacked neither understanding nor genius.

After an account of his early years, occupied in study day and night, Hartsoeker, in the posthumous work of 1730, reverts to his method of making microscope lenses—an occupation to which he was introduced by his master in Mathematics. Hartsoeker happened to be waving a glass thread in the flame of a candle, when he noticed that the end of the filament became rounded, and as he knew that a glass sphere magnified objects placed in its focus, he mounted the globule between two sheets of lead in much the

same way as he had seen Leeuwenhoek do when he was at his house with his father.[1] He was rejoiced to find himself in possession of a good microscope, and at little cost. He admits that up to the time of Leeuwenhoek no one had thought of using small globules of glass to examine transparent objects against the daylight, and he quotes the mathematician Hudde as having expressed surprise that Leeuwenhoek, a man without learning and without genius, should have led the way in this matter.

Among the objects Hartsoeker says he examined with his new microscope in 1674 (he would then be eighteen years of age) was the semen of man, in which he saw a prodigious number of little animals, but as he believed that their presence was due rather to some disease, he kept his counsel at the time, and the discovery came to naught. He then spent some years in the study of the 'false and ridiculous' Cartesian philosophy, but resumed his microscopical observations in 1677, when he again discovered the animalcules in the semen of man. They were all of the same size and shape, and resembled the tadpoles of frogs. This discovery he communicated to his master in Mathematics and to one of his friends, and as they found the same animalcules in the semen of the dog, they concluded that their presence was not due to disease, but that they belonged naturally to the semen, in which they would doubtless be found in all animals. He was confirmed in this conclusion by finding similar animalcules in the semen of the cock and pigeon, but with this difference—in the birds they resembled small worms or eels, as he had stated in 1678. When he was asked where the human animalcules were found, he replied that it was in the saliva, which mis-statement, being spread about, explains, he thinks, why Leeuwenhoek, in order not to appear to see less than his contemporaries, had described a vast number of small animals in saliva, which certainly were not there. At this time Huygens, having returned to Holland from France, and having heard of Hartsoeker's discovery, expressed a wish to see him, and at this meeting

[1] But he has only just claimed that he had learnt nothing from Leeuwenhoek.

Hartsoeker confessed that the animalcules had been found not in saliva but in the semen, and that he had had reasons for issuing a false report, although he does not disclose what they were. Hartsoeker then proceeded to Paris in the spring of 1678, where he found that Huygens' observations, made with the microscope of new construction, were being discussed.[1] These observations, and the invention of the microscope by which they were made, Hartsoeker claimed as his own, and roundly accused Huygens of plagiarism. He was urged to expose Huygens in the leading French Journal, but being ignorant of the French language, an indictment was prepared by his advisers, to which all those who had any animus against Huygens contributed. This was copied by Hartsoeker, and submitted to the Editor of the *Journal des Sçavans*, who, however, refused to publish it, but instead passed it on to Huygens. The latter again sent for Hartsoeker, upbraided him for his share in the conspiracy, and offered to draft an account of the discovery of the male seminal animalcules under Hartsoeker's own name. Hartsoeker, not unwilling to propitiate Huygens, gladly consented to this, and a few days later Huygens composed the note which was published in the Journal for August 1678, as has already been described. In this note, however, the question as to who was the first to discover the spermatozoa was not raised, but, on the evidence now available, it may be stated with confidence that neither Huygens nor Hartsoeker had any share in it.

We now reach the important part which Leeuwenhoek himself played in this investigation. It may perhaps be pointed out here that Leeuwenhoek's veracity was frequently called in question, but he had also spirited defenders, and he would occasionally produce the written testimony of people of standing to whom he had demonstrated his discoveries. He is evidently hurt by the charge, and makes frequent reference to it in his letters. His first letter on the spermatozoa, written in Dutch, the only language at his command, and dated November 1677, was translated into Latin by a friend (unknown) and sent to the Royal Society, who

[1] But Huygens' note was not published until August 15th of that year.

published it in the *Philosophical Transactions* for 1679. Of the three extant versions of this letter the Dutch one (Letter No. 113) is the most authentic, and probably represents in full Leeuwenhoek's original text of 1677. The second Latin version is a retranslation from the Dutch. No manuscripts of any of these three letters have survived, and hence the first printed text in the *Philosophical Transactions* is the original. The 'Mr. Ham' mentioned by Leeuwenhoek in this letter did not himself publish anything on the spermatozoa. He was Johan Ham, a Dutchman of Arnhem, who was born in 1650 or 1651, but the date of his death is unknown. He discovered the spermatozoa when he was a medical student at Leiden. He qualified in medicine later and practised as a doctor at Arnhem, of which town he became the Burgomaster. The Ludwig von Hammen of Danzig (1652–89), the author of the *De Herniis*, who is usually credited with the discovery of the spermatozoa, is another person who had no connexion whatever with it. This error was made originally by Haller in the seventh volume of his *Elementa Physiologiae* of 1765, and it has been copied ever since, in spite of several authoritative corrections.

Leeuwenhoek's letters on the spermatozoa do not appear in Hoole's English translation of his works, the translator evidently subscribing to the opinion that such subjects 'to many readers might be offensive'. Hence his title, 'The Select Works of Antony van Leeuwenhoek'. An English translation of Leeuwenhoek's historic letter has hitherto not been published, and may therefore be fitly given here[1]:

'The Observations of Mr. Antony Leeuwenhoek, on Animalcules engendered in the Semen [Letter No. 22].

. . . . . .

A letter from the observer to the Right Honourable the Viscount Brouncker; written in Latin, and dated November, 1677; which the Editor [Nehemiah Grew] considered should be published in the very words in which it was sent.

. . . . . .

[1] This translation has been prepared by Mr. Clifford Dobell, F.R.S., and is based on the Dutch and two Latin printed versions of the letter. 'In translating Leeuwen-

After the distinguished Professor of Medicine Craanen had himself many times honoured me with a visit, he besought me, in a letter, to demonstrate some of my observations to his kinsman Mr. Ham. On the second occasion when this Mr. Ham visited me [in August, 1677], he brought with him, in a small glass phial, the spontaneously discharged semen of a man who had lain with an unclean woman and was suffering from gonorrhoea; saying that, after a very few minutes (when the matter had become so far liquefied that it could be introduced into a small glass tube) he had seen living animalcules in it which he believed to have arisen by some sort of putrefaction. He judged these animalcules to possess tails, and not to remain alive above twenty-four hours. He also reported that he had noticed that the animalcules were dead after the patient had taken turpentine.

In the presence of Mr. Ham, I examined some of this matter which I had introduced into a glass tube, and saw some living creatures in it: but when I examined the same matter more carefully by myself, I observed that they were dead after the lapse of two or three hours.

I have divers times examined the same matter (human semen) from a healthy man (not from a sick man, nor spoiled by keeping for a long time, and not liquefied after the lapse of some minutes; but immediately after ejaculation, before six beats of the pulse had intervened): and I have seen so great a number of living creatures in it, that sometimes more than a thousand were moving about in an amount of material the size of a grain of sand. I saw this vast number of living animalcules not all through the semen, but only in the liquid matter which seemed adhering to the surface of the thicker part. In the thicker matter of the semen, however, the animalcules lay apparently motionless. And I conceived the reason of this to be, that the thicker matter consisted of so many coherent particles that the animalcules

hoek', Mr. Dobell remarks, 'it is most important to remember that he himself used nothing but the most common and homely words. All scientific or literary expressions were wholly foreign to his nature, and should not therefore be used if it is wished to represent his sayings justly.'

could not move in it. These animalcules were smaller than the corpuscles which impart a red colour to the blood; so that I judge a million of them would not equal in size a large grain of sand. Their bodies were rounded, but blunt in front and running to a point behind, and furnished with a long thin tail, about five or six times as long as the body, and very transparent, and with the thickness of about one twenty-fifth that of the body; so that I can best liken them in form to a small earth-nut with a long tail.[1] The animalcules moved forward with a snake like motion of the tail, as eels do when swimming in water: and in the somewhat thicker matter, they lashed their tails some eight or ten times in advancing a hair's breadth. I have sometimes fancied that I could even discern different parts in the bodies of these animalcules: but forasmuch as I have not always been able to do so, I will say no more. Among these animalcules there were some still smaller particles, to which I can ascribe nothing but a globular form.

I remember that some three or four years ago I examined seminal fluid at the request of the late Mr. Oldenburg, Secretary of the Royal Society. Looking into the matter I find that he wrote asking me to do so from London, on the 24th of April, 1674: and among other things, he besought me also to examine saliva, chyle, sweat, &c.: but at that time I took the animalcules just described for globules. Yet as I felt averse from making further inquiries, and still more so from writing about them, I did nothing more at that time. What I here describe was not obtained by any sinful contrivance on my part, but the observations were made upon the excess with which Nature provided me in my conjugal relations.[2] And if your Lordship should consider such matters either disgusting, or likely to seem offensive to the learned,

[1] Leeuwenhoek is here comparing the spermatozoa with the 'nuts' of the plants which form our common 'Earth-nuts' or 'Pig-nuts' (*Bunium flexuosum*). *Bunium* has a tuber-like swelling on its root, and when this is dug up it bears an associated rootlet —hence mimicking the form of the spermatozoon with its head and tail. This comparison is not only apt in itself, but characteristic of Leeuwenhoek's simple manner of expressing himself.

[2] Cf. Lallemand, 1841, p. 36.

I earnestly beg that they be regarded as private, and either published or suppressed as your Lordship's judgement dictates.

I have already many times observed with wonder the parts themselves whereof the denser substance of the semen is mainly made up. They consist of all manner of great and small vessels, so various and so numerous that I misdoubt me not that they be nerves, arteries, and veins. Nay, I have indeed observed these vessels in such great numbers, that I believe I have seen more in a single drop of semen than an anatomist would meet with in a whole day's dissection of any object. And when I saw them, I felt convinced that, in no full-grown human body, are there any vessels which may not be found likewise in sound semen.

Once I fancied I saw a certain form, about the size of a sand grain, which I could compare with some inward part of our body. When this matter had been exposed to the air for some moments, the mass of vessels aforesaid was turned into a watery substance mingled with large oily globules, such as I have formerly described as lying among the vessels of the spinal marrow. On seeing these oily globules, I conceived that the vessels might perhaps serve for the conveyance of the animal spirits, and that they are composed of such a soft substance in order that, as the humour or animal spirits continually flowed through them, they might thereby become consolidated into oily globules of sundry sizes—especially when they are exposed to the air.

Moreover, when this matter had stood a little while, there appeared therein some three-sided bodies terminating at either end in a point (as in Fig. A), and of the length of the smallest grains of sand, though some may have been a bit bigger. And these were furthermore as bright and clear as if they had been crystals.[1]'

In acknowledging this communication on January 1st, 1678, Secretary Oldenburg urges Leeuwenhoek to confirm

[1] Crystals of spermine phosphate which are formed in human semen only. The above passage is the first description of these bodies, which were discovered by Leeuwenhoek. Cf. for figures the letter of Dalenpatius.

his discoveries and extend them to the semen of animals, such as the dog and the horse, so that comparative data may be available as to the number and structure of the animalcules in forms other than man. To this Leeuwenhoek replies under the date of March 18th of the same year that he has examined the animalcules in the dog and the rabbit, and he now encloses drawings of them.

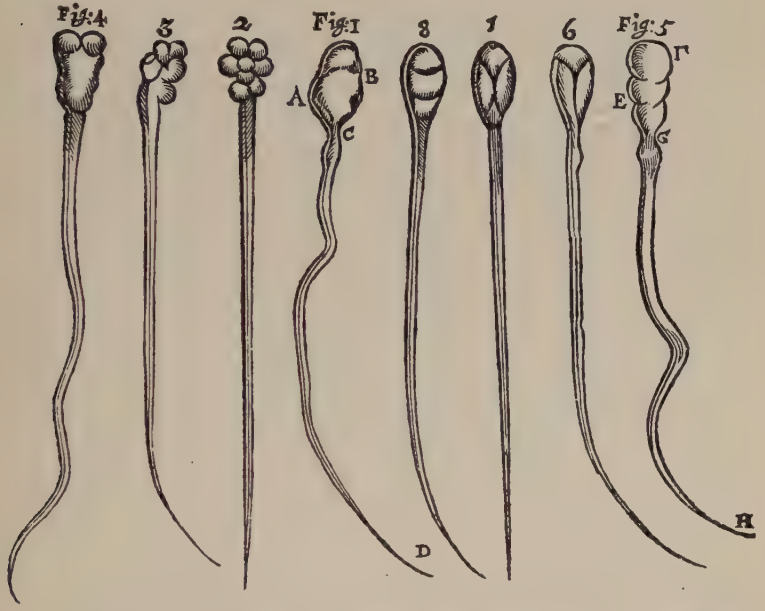

Fig. 1. Leeuwenhoek's first sketches of the spermatozoa. 1–4 are of the rabbit, and 5–8 of the dog. 1 and 5 only were drawn from living material

By 1683 Leeuwenhoek had examined the seminal animalcules in almost all classes of animals, and had substituted the theory of generation *ex animalculo* for that of *ex ovo*—a creed he continued to urge for the rest of his life. It was in fact believed that he had discovered the homunculus of Paracelsus and of the older anatomists. In man and the dog he claims to have found two kinds of animalcule corresponding to the male and female sexes—a statement he repeats in a subsequent letter. In criticizing this statement, Buffon

complains that Leeuwenhoek does not describe the differences between the supposed male and female germs, and suggests that the distinction existed only in his imagination. In a letter published in 1686, but dated 1679,[1] Leeuwenhoek mentions that Hooke had demonstrated animalcula to Charles II, who had watched them with great astonishment and expressed admiration of their discoverer. Blumenbach, in commenting on this demonstration, states that Charles II commanded the *spermatozoa* to be presented to him swimming and frisking in their native fluid.[2] The spermatozoa were discovered, he adds, 'in the semen of all animals, and what is remarkable, of nearly the same size and shape in the semen of the largest and of the smallest, in the semen of the sprat and of the whale; they could distinguish the male from the female; in the semen of the ram, they beheld them moving forwards in a troop with great gravity like a flock of sheep'.

Having, as he thought, distinguished sexual differences in the spermatozoa, Leeuwenhoek in 1699 suggests that they may be able to reproduce themselves, but that they may do so with great rapidity as in other microscopic animals he has investigated, in which case the small stages would be passed through very quickly. Nevertheless he does not believe that the spermatozoa grow, but that they are all approximately of the same size. In a later letter he thinks it possible that they may generate without pairing, like the aphis, but he does not develop this suggestion.

Three early references in the literature to the discovery of the spermatozoa must suffice to close this chapter in their history. In a letter dated May 28th, 1678, but not published until 1680, T. Bartholin, jun., briefly mentions that he had

[1] An abstract of this letter appears in Hooke's *Philosophical Collections*, No. 1, 1679, but the passage relating to the King is omitted.

[2] This incident created a deep impression, and figures repeatedly in the literature of the period. Mr. Dobell, however, informs me that it is based on a misinterpretation of Leeuwenhoek's words, and that what Hooke introduced to the king was not spermatozoa but the animalcula of infusions. The mistake appears to have been made originally by Haller (1765), who quoted Leeuwenhoek as his authority, and the story was subsequently repeated by numerous authors with additions.

been shown human semen under the microscope, and had seen that it was full of a kind of animalcula. At a meeting of the Royal Society held on July 3rd, 1679, Slare, who was introduced by Hooke, demonstrated the 'animals *in semine animalium*', which he had obtained by expressing the juices from the testis of a horse, and 'Mr. Hooke putting some of the liquor upon the plate of his double microscope, an infinite number of these small wriggling creatures might very plainly be distinguished, and were discovered and observed by most of the members, who were present'. In the same year, but later, Hooke himself attempted to find them in a lamb and a very young cock, but failed to do so. In 1681 Schrader states that the first to discover the seminal animalcula was 'my very dear friend D. Ham', who found them in the cock (?), and who told Schrader that he had examined sterile semen very carefully, and had not found a single animalcule in it, nor could he find them in the semen of old animals.

II

LATER HISTORY OF THE SPERMATOZOA

THE spermatozoa having been discovered, and their existence generally admitted, the inevitable controversy arose as to their origin, structure, and meaning. Dionis in 1698 is not prepared to accept the seminal animalcula without further inquiry, since they may arise from the small fibres of the semen after exposure to air. Lister's difficulty (1698) is that assuming human bodies to be produced from seminal animalcula, where do the latter come from? They must, he argues, be generated throughout life because they are forthcoming up to extreme old age, and yet they are constantly being used up. Can they reproduce themselves, or are they produced spontaneously? The latter possibility, he says, is rejected by Leeuwenhoek, and the former leads him into an absurd position, since to generate they must be mature, and hence they must mature twice—once in the male semen when they reproduce themselves, and again in the uterus when they develop into human bodies. Leeuwenhoek in the following year replies to this criticism, but does not attempt to meet Lister's difficulty of the two maturity periods of the animalcula. He refers to the fish which empties its soft roe completely every breeding season, and yet it fills up again with a fresh batch of milt, and he surmises that at every discharge some seminal matter is left behind which by propagation is responsible for the supply of the following year. He repeats his belief in male and female animalcules, and prefers to conclude that they can procreate their kind rather than that they are spontaneously generated. Lister returns to the problem in 1709, and now concedes that the male semen is crowded with vermiculi, but maintains that their function is merely to incite the male to perform the sexual act. He points out that the semen is not peculiar in possessing vermiculi, which occur in other regions and humours of the body, and hence they are not necessarily concerned with genera-

tion. The view that they develop into men he dismisses as absurd.

'Homunculi isti quanti sint, cum cogito,
Haec res agetur aliis, mihi certe fabula.'

The occurrence and behaviour of the spermatozoa at different periods of life was noted by many of the early microscopists. Thus Geoffrey and du Cerf (1704) observed that spermatic animalcules do not occur in sterile individuals, and in old men only a few are found, which are feeble in their movements, and they may even be absent. In a boy of twelve or thirteen years they are present in great numbers and are not fully mature, but in an individual of middle age they are well developed and exhibit great activity. All these circumstances seem to indicate that these small animalcules may nevertheless be the essential and immediate cause of generation.

Schurig in his useful compilation (1720) does not accept the spermatozoa. He says that any observer could concoct similar animalcula with a good microscope, and that Leeuwenhoek was misled by his preconceived opinions. What he regards as tailed worms are only the active portion of the semen agitated in a viscid mass, which, becoming slowly consumed, leaves behind some inactive fibres which Leeuwenhoek set up as the dead bodies of the worms. A new attitude is adopted by Vallisneri (1721), which had important bearings in the subsequent discussion. He confirms the existence of the animalcula, but holds that their object is to prevent the clotting of the semen and to keep it fluid. They have no relation to actual generation itself—in fact he regards them as simple independent organisms or parasites.

In an important work on the development of the Chick (1722), Maître-Jan admits that he was unable to find the spermatic worms himself in the dog, cat, cock, and bull—a failure he attributes to the defects of his microscope. He does not, however, deny their existence, but suggests that if they really exist, there is no reason to associate them with any essential process of generation. On the other hand, Folkes, in the course of his description of Leeuwenhoek's

microscopes (1724), refers particularly to 'that famous discovery of the animalcula *in semine masculino*, which has given a perfectly new turn to the theory of generation in almost all the authors that have since wrote upon that subject'. Gesner (1737), a philosophical writer, accepts the statements of Leeuwenhoek and Hartsoeker on the seminal animalcula, which he says leave no room for doubt. He describes the discovery as an 'incredible marvel', and the object of his paper is to transfer the credit of it to Hippocrates, who, by the sole force of his reason, discovered what only the best eyes backed by the best microscopes can perceive. The proofs of this contention depend on taking various trifling liberties with the text, including the translation of *ψυχή* as animalcule. With such methods at command, there are no limits to the discoveries which may be found in the writings of the ancients.

When Linnaeus was staying in Leiden in 1737, he attended the microscopic demonstrations of Lieberkühn, and at one of these the animalcula *in semine masculino* were exhibited. He at once declared his conviction that these moleculae were not true animalcules, but inert corpuscles, and he published this opinion later in 1746. He therefore opposed Leeuwenhoek's *ex animalculo* theory, and did not afterwards change his mind.[1] The French naturalist Lyonet, celebrated for his superb studies on the anatomy of insects, discusses the spermatic animalcules in his edition of Lesser's *Insecto-Theologia* (1742). He denies that the semen of all potent animals has animalcula. They may be absent, and the individual so deprived be still potent. He argues that they may be the result of fertility and not the cause of it, i.e. the fertile semen alone may possess the quality essential for the multiplication of the animalcula, whereas the sterile semen may be an unfavourable medium. For example, 'a species of small serpent is often generated in vinegar, but never in the wine from which that vinegar has been made; must we therefore conclude that it is the existence of these small

[1] Linnaeus' views on the spermatazoa are severely criticized by Spallanzani (1776).

serpents which differentiates vinegar from wine? Rather should we not believe that they are found in vinegar because it alone is a suitable medium for their life and multiplication?' He maintains further that the animalcula are found in all parts of the body, such as the skin, blood, mouth, and faeces, where they can hardly be supposed to have any relation to generation. He regards them as parasites, but not necessarily as harmful. The interpretation of the spermatozoa as entozoa, which was first suggested by Vallisneri, is thus adopted by Lyonet as a plausible hypothesis.

Maupertuis (1744) admits the existence of the spermatozoa, but is unable to demonstrate the use of them. He proposes an explanation which is somewhat similar to that suggested by Vallisneri—that by their movements they serve to keep in agitation, and in that way to mix completely, the two seminal liquors. James (1745) admits that the spermatic animalcula 'really exist, and are easily visible by the help of glasses', but since they are never to be found in the fresh uncorrupted semen, they must be interpreted as one of the products of putrefaction. Leeuwenhoek's new system of generation is 'utterly romantic, and inconsistent with the conduct of Providence, observable in all natural productions'. A somewhat analogous view was expressed in 1746 by Wahlbom, who described the seminal animalcula as inert oleaginous corpuscles set in motion by the heat of the semen, and another variant is that of Procope Couteau (1748), who believed that they originated during the sexual act, and perished on its completion.

It is now necessary to give some attention to the experiments and speculations of Buffon (1749, 1777), described by Haller as that great man who only embellished with the eloquence which was natural to him the system of Democritus and Hippocrates, but, says Dalyell, 'we descend from the observations of Leeuwenhoek to those of Buffon'. The great French commentator and naturalist examined the spermatozoa of man, dog, rabbit, ram, and fishes. They possess, he claims, no characteristics of animality—they are not little animals. He ranks them among his aggregates of

'living organic molecules', and derives them from the mucilaginous parts of the semen and its filaments, which can be seen undergoing conversion into spermatozoa under the observer's eye. Hence they are formed outside the body, and, not only so, but they actually increase in number, size, and activity after they have left the generative organs. The semen when first discharged is generally full of branching filaments. From these filaments the spermatozoa are derived, and at first possess tails. They become detached from the filaments, and move about slowly, being encumbered by their tails, which are not swimming organs but accidental appendages.[1] The tails are then lost, and motion becomes much quicker. They may now change their shape and size and divide by fission. Buffon positively asserts that in 1748 he had found, and demonstrated to Daubenton and Needham, spermatic animalcula in the Graafian follicles of a bitch in heat which had never been covered—an assertion as positively denied by Gleichen and other contemporary observers. In a letter dated November 1776, but not published until 1860, Buffon returns to the subject. He has evidently not changed his views, which in fact are restated in his volume of 1777. The microscope, he says, has produced more error than truth. He accepts none of the 'pretended discoveries of M. Spallanzani', and is surprised that any one should believe that the spermatic worms and those of infusions are true animals recognizable as species different from each other. Nothing is less proved or more false than this assertion. He had seen the so-called spermatic animals a long time before Spallanzani, but regarded them as nothing but the first aggregates of the living organic molecules. Buffon need not be taken seriously as a microscopical observer, and his views on the spermatozoa are so similar to those of Needham, which were also published in 1749, that it is impossible to disregard the significance of the coincidence.[2] According to Needham, the spermatozoa are

[1] Cp. Needham, 1749.

[2] Compare the Preface to the French edition of Needham (1750), in which he explains how his results were made use of by Buffon to illustrate the theory of organic molecules.

'organized bodies' which are produced in that exalted medium called the semen by a combination of active principles. After the semen is discharged it liquefies, vegetates, and shoots out filamentous ramifications, which latter break up to form the spermatozoa. The spermatozoa therefore do not form a part of the original semen, but arise later—it may be immediately after discharge, or not for some hours. The tails of the animalcula, so far from assisting locomotion, impede it, and produce an unstable oscillatory movement. They are, in fact, long filaments of the viscid seminal substance which is trailed after the moving globule. The animalcula play no essential part in generation, but are a by-product of the operation of those particles in quest of organization, which are themselves the true and adequate cause of it.

In 1751 Lieberkühn, who was an animalculist, develops a suggestion which may be described as the natural outcome of previous observations. He attempts to prove that the form of the spermatozoa fits in with the type of adult into which it is to develop. Thus the sperm of the snail, which has no backbone, has a long slug-like structure and moves accordingly. Again, the tortoise has no movable backbone (which is fused with the shield) but has a mobile neck, and hence its spermatic animalcule has the tail in front and not behind. Nevertheless the animalcule does not move backwards, but is pulled forwards by hooking movements of the tail.

The first author to classify spermatozoa as distinct animals, and therefore to label them definitely as Infusoria or Parasites, is Hill (1752). He puts them in the group of 'Lesser animals called animalcules' alongside *Vorticella* and (?) *Euglena*, and treats of the spermatazoa of various Mammals including Man, Amphibia, Reptiles, and Insects, but his descriptions are too vague to make it possible to identify the forms he is describing. He places them under his new genus *Macrocercus*, and there are six species. In the English translation of Swammerdam's *Biblia Naturae* (1758), there is a note presumably by Hill in which it is stated that the

'animalcules in semine' are more easily and distinctly seen in the sperm of the male frog than in any other way. 'They who doubt the existence of such animalcules (for it is at present a fashion to doubt them) have not examined the male sperm of this creature.' The fashion referred to by Hill is exemplified by Ramström (1759), a pupil of Linnaeus, who followed the lead of his teacher, and questioned the status of Leeuwenhoek's seminal animalcula. They are, he says, not animals, but floating oleaginous particles of lifeless matter suspended in a liquid and put in motion by heat. His material was obtained only from the dog. At the time Ramström was writing it was well known that the spermatozoa of the frog were active, although heat could play no part in their activity. Astruc, in his lectures of 1740, and later in his treatise of 1765, accepts Leeuwenhoek's descriptions of the spermatozoa, and on the grounds that they are not found outside the male genital humour, that they are either not present in very young males or if present exhibit no movements, and that they become very active during the period of propagation and revert to the languid condition in old age, he concludes that they must constitute an important element in generation, and indeed defends the animalculist position. The vermiculi, he says, are either male or female, the former being the larger, and whilst those of the same species differ only in size, specific characters may be detected in different species.

The preconceptions of Haller would not dispose him to attach much importance to the spermatozoa. Their discovery, he remarks, produced a great stir. They were shown to King Charles II,[1] they were talked about everywhere, and accepted almost by all—in fact this discovery enjoyed as much celebrity as an incident of such elementary importance could deserve. He admits that he has not found the animalcula in infants, young lambs, sterile animals, old men, and mules. Nevertheless they belong naturally to the semen, and form its essence. They are found in all animals, and are not derived from the air, or they would occur in all

[1] But cp. p. 14.

animal humours. On the other hand he regards as pure conjectures the following statements of Leeuwenhoek and others: that they have sex; that they copulate and reproduce themselves; that small and immature specimens occur; that they moult their skins and tail; and that they may have two heads. Certain writers, he adds, especially those in the last century, thought they saw things the reality of which is open to grave question, and it is only with the greatest reserve that one can admit even what the most celebrated men have written.

One of the earliest naturalists actually to examine the spermatozoa as well as to write about them is Spallanzani (1776).[1] He amply confirms the observations of the 'most accurate Leeuwenhoek', and firmly opposes those of Buffon. He denies the formation of the spermatozoa outside the body from the solid or filamentous part of the semen, and demonstrates that typical tailed examples occur in the fluid part of the semen even when it is included in the organs of generation. They do not multiply by division. He suggests that Buffon was dealing for the most part with the organisms of putrefaction, and may not have seen the spermatozoa at all. When Buffon describes the loss of the tails of the animalcula, he had probably only observed their death and the appearance of tailless infusion organisms. Spallanzani himself, however, has no clearly defined views as to the real nature of the spermatozoa. He professes to have found them in the blood,[2] and thinks they might originate there. He does not detect any signs of complex structure in them, and concludes that they must be ranked among the normal constituents of the animal kingdom. In a letter to Spallanzani dated 1771, Bonnet comments on Spallanzani's work on Infusions, and adds: 'Your observations [on the spermatic

[1] It is interesting to note that Spallanzani preferred the simple to the compound microscope when investigating the spermatozoa. He remarks that it is a fact acknowledged by all observers that the single lens gives a better defined picture than the compound microscope.

[2] Gruithuisen (1812), who held that the spermatozoa propagated by longitudinal fission like the Infusoria, and even by budding, also claims to have seen them arise in the blood.

worms] have a great value in my eyes—they are both new and exact. I wish we could resuscitate the good Leeuwenhoek. What a pleasure it would have been to him to find himself avenged for the attacks of Buffon.' Gleichen (1778), like Spallanzani, approaches the problem of the spermatozoa from the microscopic side. He holds that, apart from the witticism of Dalenpatius, they have been in the main accurately described by those who have made a proper microscopic examination of them, and he expresses surprise and indignation against those who have doubted their existence. He emphatically disputes Buffon's assertion that animalcules similar to spermatozoa are to be found in any of the secretions of the female, and is equally emphatic that they should not be confused with the infusion organisms, since they have an entirely different origin.

In 1779 Blumenbach, like Hill, refers the 'animalcula found in the semen' to the Infusoria, but he describes them under the new name of *Chaos Spermaticum* (*Cercaria spermatica*). In 1780 he develops this view in the following passage: 'I cannot conceive how some professed philosophers and natural historians have been led to deny life and voluntary motion to those animalcula [spermatozoa], but I am still more at a loss to imagine how another set of philosophers have been induced to dignify these animalcula of a stagnant animal fluid to the high rank of the organized germs of successive generations.' His objections to the latter attitude are: (1) nearly related animals may have very different spermatozoa, and conversely widely differing animals may have almost identical spermatozoa. For example, the sperms of the frog and newt are widely different, whilst those of man and the ass are identical; (2) more than one kind of sperm may appear in the same drop of semen, and the sperms of the same animal have been represented differently by various authors. Their form, therefore, is irregular and uncertain, which would not be the case if they were foetuses.

Senebier (1785) confirms the suggestion of Spallanzani that Buffon confused the spermatic worms of animals with the widely different organisms which appear in the semen

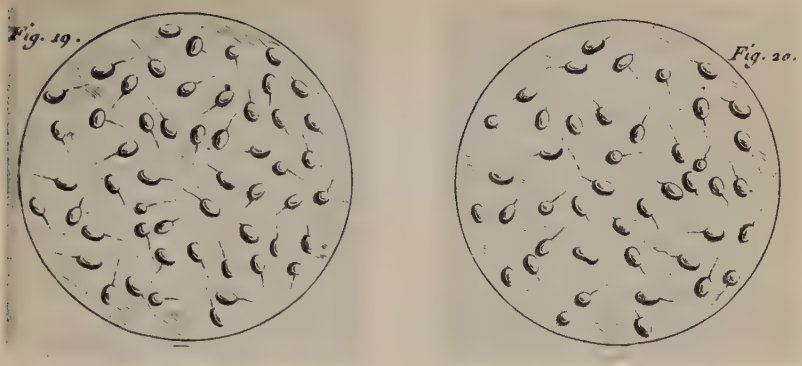

Fig. 2. Buffon's figures of 'spermatic animalcula' from the seminal liquor of a dog (19) and from the Graafian follicles of a bitch (20) to establish the identity of the two substances

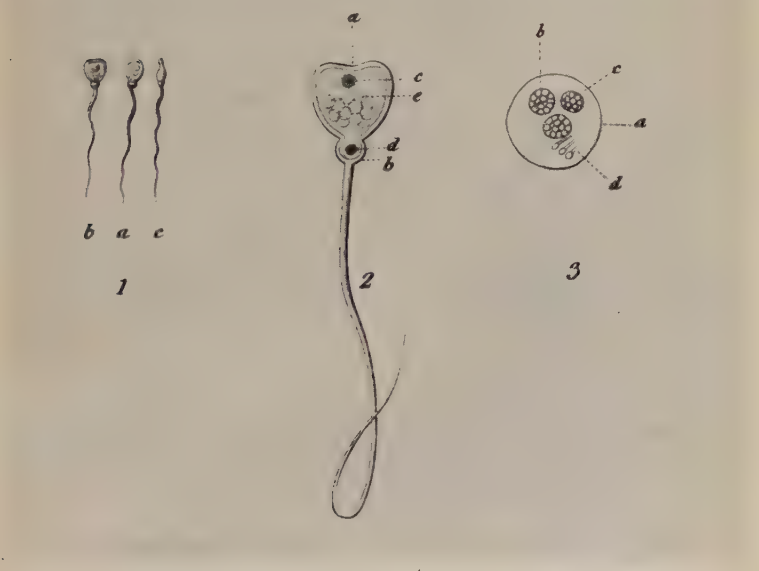

Fig. 3. Valentin's figures of the early and mature stages of the spermatozoa of the Boar

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subsequent to putrefaction. He also criticizes Leeuwenhoek for his belief that generation is effected only by the spermatic worms, but he says 'undoubtedly this error is that of a great man'. It illustrates, he continues, the danger of giving rein to an imagination which betrays one into beliefs which are not even probable. The spermatic worms have been much studied since Leeuwenhoek, but it must be admitted that their purpose in the seminal fluid is nevertheless unknown. That they are not essential to generation, he adds, has been proved by the penetrating genius of Spallanzani, who fecundated the eggs of a toad with seminal liquor which contained no spermatic worms. This statement, however, was negatived by Prévost and Dumas (1824), who asserted that if the male seminal liquor be filtered, the filtrate is deprived of its fertilizing power, but that the residue retains it. Hence the virtue lies in the animalcula, which exercise a real and perhaps an exclusive influence in the act of generation. They have no points of similarity with the Infusoria, and are not parasites, but represent a true product of the genital gland in which they are found. This important paper contains the first tentative suggestion of the histogenesis of the spermatozoa in the tissues of the testis, and a clearer appreciation of the part taken by the sperm in fertilization than is to be found in any previous publication. Treviranus was in 1805 unconvinced by Leeuwenhoek's spermatic animalcula, but later, in 1833, in contesting the belief that they are parasites comparable with infusion organisms, he advances a novel and interesting proposal of his own. He regards them not as distinct or independent animals, but as bodies *analogous to the pollen of plants*. The tails represent the connexions of the animalcula with the surface of the secretory vessel in which they are formed, and when they are detached they carry the connecting fibres with them. He proposes therefore to call these bodies 'animal pollen', and their activities are not considered to be spontaneous, but as similar to the so-called Brownian movements. In this work we find another hint of the origin of the spermatozoa from the tissues of the reproductive organ.

Bory de Saint-Vincent (1824) was not able to distinguish any structure in the zoosperms,[1] even with the most powerful microscope at his disposal. There are no articulations in the tail representing a vertebral column, as other hasty observers had described, and the expanded part is not the rudimentary head of a larger animal. He contests the statement that the zoosperms are cercariae,[2] from which they are distinguished by their lateral compression. In putrefied semen there is no life, nor has it the power of generating life, whilst the fresh semen swarms with zoosperms, and is potentially generative. He states definitely that the zoosperms are secreted in the testis, and therefore cannot be parasites, but they find in the animal body their nourishment and a habitat suitable to their organization. That is all. The function of these organisms is to ensure the mixture of the various substances necessary for generation. If they are absent the mixing does not take place, and the semen perishes without fruition. To hold, however, that they constitute the fecundating element of the semen is a hazardous idea which has never been established. Three years later (1827) Bory partly recants and partly develops his views. He now holds that the zoosperms are Entozoa and constitute 'un genre de la famille des Cercariées, dans l'ordre des Gymnodés et de la classe des Microscopiques'. They occur only in the spermatic liquor of male animals, in this respect differing markedly from other Cercariae, and Buffon is quite in error in stating that they are found in the female sex. There can be no question of their reality, but the consequence of attributing to them an importance which they do not possess only raises doubts as to whether they exist at all. Nevertheless their presence is indispensable to generation. They appear only in the adult semen at the onset of puberty, and they disappear in old age when the faculty of reproduction has been lost, nor do they exist in the sterile mule. During

[1] The colloquial term zoosperme (spermatozoa) was first employed by Bory in 1823. The genus *Zoospermos* was instituted by the same author in 1827.

[2] O. F. Müller apparently never saw spermatozoa himself, but compared them with the genus *Cercaria*, without however claiming relationship between the two.

the active reproductive periods they develop and multiply greatly. These facts point to an intimate connexion between the zoosperms and fecundation. His present conclusions, which he says are only provisional, are that the zoosperms are actually animals but are not produced by secretion. That organisms can be generated in this way is not in reason. The zoosperms develop in the semen of males just as Entozoa do in the mucous parts of other regions of the body, and they only appear when the male semen has attained the physical status necessary for their existence. He has little to add to his former opinion of their function except that in virtue of their prodigious numbers and activities they are responsible for the sexual orgasm, and also that they indirectly promote fertilization by sweeping the spermatic liquor towards the egg. In an article published later (1830), he adopts a more confident tone. The odd and verbose disputes which have been waged over the zoosperms, he says, are now at an end. The zoosperms are an indispensable element in fecundation, and their animality is beyond question. They appear to exercise will in their movements like the tadpoles of frogs.

Dumas, writing in 1825 before the publication of Bory's second article, severely criticizes Buffon's researches on the spermatozoa. They were not, he says, sufficiently extensive to justify the bold conclusions which were drawn from them. Further, his microscope was apparently unequal to work of so refined a character, and 'our Pliny' himself was not sufficiently familiar with its use. He holds that the spermatozoa are the product of a true secretion of the testis, and that they constitute the essential and indispensable factor of the male seminal fluid. This is proved beyond the least doubt by numerous filtration experiments, in which the effect of the presence or absence of the spermatozoa can be estimated.

The views of von Baer on the spermatic animacula will be scrutinized with interest, but they are disappointing. He says in 1826 that the animalcula develop in the semen only when it has acquired its highest degree of perfection, i.e. when it is very decomposable and particularly suitable for fecundation. They are Infusoria-like parasites or Entozoa of

the semen, and have no essential connexion with the life of the host, and hence can play no leading part in the process of generation, although they may be accessory or complemental to it. In 1827 von Baer was the first to fix and epitomize the parasitic interpretation of the spermatic animals by naming them *Spermatozoa*. He thinks they may be a very simple variety of the Cercaria type. They evidently have no mouth opening, and hence must represent a lower level in the scale of development than the typical *Cercaria*. Cloquet (1827) also regards the spermatozoa as Cercarias, basing his opinion on their structure. He was greatly impressed by their discovery, and remarks that of all the discoveries made by the microscope none is more worthy of attention. The complex movement of these organisms, in which volition is exhibited, are very similar to those of tadpoles—in fact they are more like independent organisms than many animals which are more highly organized. He expresses no opinion on their function, and leaves theorizing to those who have an affection for final causes. He mentions, however, that small portions detached from the gills of mussels behave like spermatic animalcula, which is an early, but not the first, mention of ciliary action. Home's contributions to the theory of generation (1828) are not impressive. Apart from a detailed description of a uterine 'human ovum', which is apparently the egg of a blowfly, his views on the spermatozoa, based on an investigation of the deer in Richmond Park during two seasons, show how far he is from even a distant appreciation of the realities of the problem. He refers to the wild theories concerning the male semen accredited at his time, and complains that Leeuwenhoek's statements on the seminal animalcula, although completely misguided, have never been fully exploded. He concludes 'that the appearance of living animalcula in the semen is not a real one, but is the effect of microscopic deception'. A year later the botanist Reichenbach was classifying blood corpuscles and spermatozoa as independent organisms, constituting the first family of the animal kingdom.

In 1833 Blainville was still discussing the classification of

the spermatic Infusoria into genera and species, based largely on the structure of the tail, a system of which he does not approve. Spermatozoa, he says, have no intrinsic powers of movement, such movement being due to the warm solvent action of the liquid in which they live. If the temperature is reduced the solvent action is weakened, and the movements either cease or become feeble. He questions the importance of the spermatozoa in generation, and even doubts their independent existence. If they are compared with genuine microscopic animals considerable differences are at once apparent. On the other hand Czermak, in the same year, after referring to the fact that very reliable observers have attached little importance to the spermatozoa in the generative act, is himself inclined to support Prévost and Dumas, and to regard the animalcula as the active principle of the semen. Delle Chiaje, however, another contemporary writer, favours a parasitic interpretation, but prefers to classify the spermatozoa as Pseudhelminthes and not as true Entozoa. Owen (1835) is also dubious. He says it is still undetermined whether the spermatozoa correspond to the pollen of plants or whether they are independent organisms, but he has decided to range them provisionally with the parasites as members of the class Entozoa of the order Protelmintha. He describes the human spermatozoon under the name of *Cercaria hominis*. He admits that no mouth or genitalia have been detected in them, but he is not prepared to deny that they are oviparous, or that they may propagate by fission. Their constant occurrence would indicate that they are concerned in the economy of the animal in which they exist.

A remarkable addition to the literature of the spermatozoa was made by Peltier in 1835–8—a contribution all the more striking since it immediately preceded the enunciation of the cell theory. Peltier was indeed the first observer to produce evidence against the parasitic interpretation of the spermatozoa. According to him they arise by the segregation and growth of elements which belong by inference to the tissues of the animal in which they are found, and if this be

so it must be conceded that the spermatozoa are not parasites. At the same time, in 1837, Dujardin reached a somewhat similar point of view. He regards the spermatozoa as a *product of the lining of the seminiferous tubules*, in which life is inherent, just as cilia still continue to move in a portion of the gill removed from a mussel. He denies that a complex structure can be detected in them, and asserts that they differ from the Infusoria in their capacity to resist decomposition almost indefinitely, whereas the true Infusoria decompose rapidly after death. He rejects the numerous interpretations of the economy of the spermatozoa which had been put forward, without being able to reach any conclusions himself, and refers particularly to the speculation that the spermatozoa have no reality, but depend on an illusion produced by the mixture of two liquids of different densities. In the same year Wagner gives a good description of the spermatozoa in all classes of animals. He attempts to work out their histogenesis, and states that they arise in clumps from vesicular shaped bodies, but does not succeed in tracing their exact origin. Each species of animal has its own, and only one, kind of spermatozoon, and each group possesses its own type, the members of the group having variants of the group type. Thus the Mammals adhere to the Cercaria and the Birds to the linear model, whilst the bony fishes have the small globular type with a very long thin tail. Without the spermatozoa the semen has no fertilizing power, for this power is lost when they are dead, and their function may be to act as the bearers of the energizing properties of the semen.[1] As might be deduced from his theoretical bias, Ehrenberg (1838) is disposed to detect traces of an internal organization in the spermatozoa. His own unpublished observations on animals of every class, he says, put it beyond all doubt that the true spermatozoa cannot be distinguished from the cercariae in the liver of the Snail.

[1] In 1836–7 R. Wagner made the important and significant discovery that the grape-like organ in the liver of Pulmonata produces both eggs and sperms, and that therefore in these animals the ovary and testis are combined to form a single organ. He did not determine, however, whether *ripe* eggs and sperms occurred simultaneously in this ovo-testis.

An interesting but extraordinary mistake was made by Carus in 1839. He describes the spermatophores of Cephalopods as independent organized animals having large and small intestines, stomach, and oesophagus—a most curious instance, remarks Eschricht, of the predilection of parasites for certain localities. In spite of the fact that a correct description of these bodies, as far as it went, had been published by Needham in 1745, J. Müller, in his Text-book of Physiology issued some ninety years later, accepts Carus's account, and still considers it doubtful whether the spermatozoa generally are independent parasites or animated particles of the organisms in which they are found. Allen Thomson (1839) writes in much the same vein. 'There is good reason to believe', he says, 'that the existence of seminal animalcules in the male product is in some way or other intimately connected with the integrity of its fecundating property; if not, as some are inclined to hold, the essential cause of it.' He is, however, unwilling to come to any general conclusion regarding the nature of spermatozoa, nor is he convinced that they occur only in the male semen. They bear a close resemblance to some of the Infusoria, and have as good a claim to be considered independent organisms. Nevertheless they are invariably present in the male semen, and must be regarded as natural constituents of it, but it is not yet proved that they are the active or indispensable agents in fecundation. A much sounder view is taken by Lallemand (1840–1). The spermatozoa, he says, have no internal organization, nor is there any reason to believe that they are parasites. They are formed in the substance of the testis just as the eggs arise in the interior of the ovary. The spermatozoa are tissue elements, they represent detached organized and living fragments of the tubules of the testis, and are *not* formed, like the seminal liquor in which they float, by secretion. The essential function of the testis is to produce the spermatozoa. Lallemand produces evidence that the spermatozoa do actually arise from the walls of the seminiferous tubules, but no histological proof is offered of their precise origin from the cells of the testis. He therefore

shares with Peltier and Dujardin the credit of having recognized the real status of the spermatozoa, the demonstration of which was provided by Kölliker in 1841.

A final attempt to establish the existence of a visceral apparatus in the spermatozoa by microscopic observation was made by Valentin (1839), Gerber (1840), and Pouchet (1847). Leuckart in 1853 remarks: 'The belief in the animal nature of the seminal corpuscles was so deeply rooted that even many practised and eminent microscopists, such as Ehrenberg, Valentin, Gerber, Schwann, and others, attempted to demonstrate in a homogeneous substance the presence of a more or less complex organization.' Valentin, in spermatozoa taken from the vas deferens and epididymis of an old boar (Fig. 3), distinguishes a mouth and anus, and an internal structure which is interpreted as stomachs or a coiled gut. In the testis he found an earlier spherical stage, with contained tailed bodies, which he thought might be the embryos of the spermatozoa. These statements were sharply criticized by Kölliker, Dujardin, and others, but Berres in 1843 was still attempting to demonstrate a gut and an ovary in the spermatozoa of Man. Gerber investigated the spermatozoa of the Guinea-pig. He distinguishes a ventral or abdominal aspect, an anterior papilla with an oral aperture, and an anal papilla with a rounded anal orifice. The anterior two-thirds of the body is occupied by globular vesicles similar to the stomachs of the polygastric Infusoria,[1] and the posterior third exhibits two rounded bodies which are interpreted as sexual organs. He considers that the spermatozoa are propagated by ova, and that they are parasitic Entozoa. He is aware, however, that the seminal fluid without these 'Entozoa' is incapable of fertilizing the ovum, but, notwithstanding this,

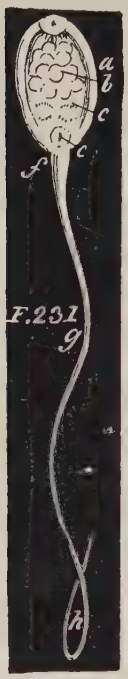

Fig. 4. Gerber's figure of the spermatozoon of the Guinea-pig

[1] Ehrenberg's polygastric theory was exploded at about this time.

Fig. 5. Human spermatozoa, after Pouchet, very greatly magnified

a. Anterior buccal apparatus followed by the vesicle and the coiled intestine. The whole surrounded by an 'epithelial' pellicle

b. Specimen which tore the epithelial pellicle into shreds after prolonged struggles

c. Specimen which has thrown off the epithelial pellicle posteriorly in one piece. This condition, which has been previously described but not understood, 'occurs frequently'

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he declines to express the opinion that they are essential to the generation of the host.

The ardent temperament of Pouchet, to which he surrendered without a struggle, was not calculated to prevail in an investigation which would have taxed all the faculties of a critical and constructive mind. He opens (1847) by assuming that there *must* be organization in the spermatozoa, and this, he says, may be interpreted either as the beginning of the foetus, or as the parts of a parasitic animal which has no direct concern with the generative process of its host. He takes the latter view, and it is characteristic of the attitude which Pouchet invariably adopted that his alternative would have led him into a trap no less disastrous. The following are his main points. Sufficient is known of the spermatozoa to make it possible to determine their essential nature, and to refute the numerous hypotheses which have sprung up around them. They are undoubtedly animals, and reproduce themselves in the special manner characteristic of the Microzoa. They have certain internal structures which may correspond to viscera, they possess a definite organ of locomotion—a true fin, and their movements postulate an undoubted volition. After this who can contest their animality? They are entirely surrounded, body and tail, by a kind of epithelial envelope which has been 'positively perceived', and is 'so manifest' that individuals may be found which have recently moulted it—a process which may be compared with the similar phenomenon in Insects. This envelope is not homologous with the epithelial layer in higher animals, but it has a granulated surface which would indicate that 'it consisted probably of cells'. Although habituated to microscopic observation, and having excellent microscopes, it was only, he says, by prolonged and persevering studies that any traces of internal organization were recognized in the spermatozoa, but at last after many failures some individuals were found to possess a complex structure, and hence their animality was revealed. There is an anterior nipple which may be a mouth or sucker, and here also, in the cephalogastric enlargement, is a vesicle

occupying about a third of its cavity. This vesicle is transparent, and thus appears as a bright area. It may be a stomach, or a suctorial apparatus such as is found in some biting Insects. Behind it is a brownish spot which may be interpreted as a visceral mass, since in it may be vaguely recognized a convoluted intestine. 'If there is growth there must be nutrition, and if there is nutrition there must exist an alimentary apparatus.' The number of naturalists who have described the internal organization of spermatozoa may be small, but it cannot be doubted that their number will be rapidly augmented in the near future. Thus several observers have denied a complex structure in the Infusoria, but the beautiful researches of Ehrenberg have nevertheless triumphantly established the existence in some of them of numerous stomachs.[1] 'It is probable that the zoosperms, after having experienced the same vicissitudes, will also be accorded the same justice.' When it is considered that they undergo growth and enlargement, that they have characteristic shapes, that their movements are voluntary and not mechanical, inasmuch as they move in definite directions, retire before obstacles, collect together and separate, exhibit preferences, rotate and use the tail like an oar, it is impossible to compare them with detached fragments of tissue, and to refuse to admit that they are complete independent organisms.

Pouchet does not discuss in detail the origin of the zoosperms, but he evidently holds that they are produced *in situ* by heterogenesis, without which he says it is impossible to explain the occurrence of certain parasitic worms in the internal cavities and solid tissues of the body. He is acquainted with the work of Kölliker (1841), but entirely fails to appreciate the significance of it. Instead of recognizing that Kölliker was attempting to demonstrate the histogenesis of a normal tissue element, he concludes that the opposite is established, and that the origin of the zoosperms is ascribed to heterogenesis. Pouchet's general conclusions on the zoosperms are: (1) they possess an internal structure; (2) their development is analogous to that of

[1] Ehrenberg's polygastric hypothesis was dead when Pouchet was writing.

certain independent organisms; and (3) their movements are controlled by volition. Hence he regards them as true animals, but he does not attempt to classify them, or to determine their zoological status.

In the first edition of the *Règne Animal* (1817) Cuvier includes the spermatozoa, on which animalcules 'so many bizarre hypotheses have been founded', under the genus *Cercaria*. Cuvier, however, was apparently not interested in the genus and says little about it—in fact he discounts the general importance of the male semen, and holds that in many species there is no need for a true fecundation. In an important and critical paper Eschricht (1841) rejects the parasitic interpretation of the spermatozoa, and holds that in view of the establishment of several very important new facts, such as the 'gradual and regular development of the spermatozoa in small sacs', it has been proved that they are 'essential parts of the seminal fluid', and 'must be considered as analogous to the globules of the blood. Their apparently voluntary motion by no means warrants the inference that they are distinct animals'. He denies, further, that any internal organs can be established in them, nor is there any evidence that they can propagate their own species. In *Ascaris* the genital organs and their products in the two sexes tend to resemble each other in their anatomical relations, and hence *the spermatozoa may be comparable with ova.* This paper, published in the same year as Kölliker's famous thesis, plainly indicated that the morphological significance of the spermatozoa had at length been perceived, and that the needful confirmation of the suggestion by the cytologist might materialize at any moment.

Following hard on the institution of the cell theory, of which it was one of the first and most striking results, was the demonstration by Kölliker, in 1841, that the spermatozoa were not organized parasites, but motile histological elements or modified cells, which arose as integral parts of the organisms in which they occurred. He named them *Fila spermatica*, and by tracing their histogenesis from the cells of the testis in the supposed host settled once and for all the first of the

great problems which these inconspicuous but tremendous particles have presented to the human mind.

A few years after the publication of Kölliker's paper, in 1849, Wagner and Leuckart are in a position to assert authoritatively that the spermatozoa of the male are normal constituents of the animal organization like the ova of the female, and are as necessary to the semen as the blood corpuscles are to the blood. Their remarkable movements are no proof that they are independent parasitic organisms, since this motion is paralleled in other animal and plant structures, the normal status of which cannot be questioned. The liquor seminis is probably an unimportant and incidental element of the semen, the object of which is to hold the spermatozoa in suspension. Of the function of the spermatozoa themselves nothing certain is known beyond that in some way by their contact they fecundate the ovum. The *nature* of the spermatic animalcula having thus been discovered, an approach was opened for an attack on the precise role which they play in the generative process.

III

FIRST STATEMENTS OF THE PREFORMATION DOCTRINE

'The old evolution [preformation] was the greatest error that ever obstructed the progress of our knowledge of development.' Whitman, 1894.

THE preformation doctrine, as a philosophical conception, has its roots in antiquity. It has also relations with theological dogma, in which it takes its place as an essential factor in the original scheme of creation. Empedocles and Plato, and the Fathers of the Church, alike regard it as a part of their system. Aristotle, however, is of another mind, but although he argues against the animal existing ready-made in the semen, in proof of which he cites his own observations on the development of the chick, the lack of any means of checking such a belief compels him to speak rather as a philosopher than as an embryologist. He held that the generative principle resided in the male semen, and that the female semen served only for the nutrition and expansion of the foetus. The male therefore was responsible for the form (efficient cause), and the female provided the substance (menstrual blood). As the rhetorical Buffon puts it: 'the male semen is the sculptor, the menstrual blood is the block of marble, and the foetus is the figure which is fashioned out of this combination'. If Aristotle had known of the spermatozoa he would probably have been an animalculist. In the *Historia Animalium* Aristotle says that 'in a certain district of Persia when a female mouse is dissected the female embryos appear to be pregnant', which reads very like the statement of a seventeenth-century evolutionist. The modern disciple of the old Preformation, with whom alone we are concerned, is in a different position. He claims, or at all events hopes, to establish the doctrine on the enduring basis of observation, and such a claim can no longer evade the searching arbitrament of the microscope.

A good example of the works on generation produced

before the period of serious research is to be found in the essay of Lemnius or Levinus (1559), the famous physician of Zirizea. It has no scientific value, but it represents fairly the collection of gossip and abject superstition which passed for knowledge at the time. The uterus is regarded as the 'till'd ground for to sow the seeds on'—a popular idea, based obviously on the analogy with plants, which prevailed long before and after this period. The seed of the male is therefore the chief agent in generation, but cannot produce an embryo without the co-operation of the female, and whether the result is male or female depends on which side of the uterus the seed falls, the time of the year, temperature, and the incidence of menstruation. Many animals are bred without seed, and arise from filth and corruption, such as mice, rats, snails, shell fish, caterpillars, moths, wasps, weevils, frogs, and eels. This agrees somewhat with the opinion of Paracelsus, who held that all generation is controlled by putrefaction. For example, there is a mucilaginous humour in eggs which by any kind of moderate continual heat is putrefied and turned into a living chick. A chick may be burnt to a powder, converted by putrefaction to a mucilaginous flegm, which if enclosed in its former shell may again be brought to maturity and form a chick. 'This is to revive the dead by regeneration, and clarification, which is indeed a great, and profound miracle of Nature. According to this processe may all Birds bee killed and made alive againe, and made new: and this is the highest and greatest miracle, and mystery of God, which hee ever discovered to mortall man.'

The first modern writer to claim that the rudiment of the embryo is actually visible in the egg before incubation is Joseph of Aromatari. Harvey, in his work on generation, mentions having visited this 'learned physician' in Venice in former years. In a short letter of three pages of print dated October 31st, 1625, Joseph mentions a work on generation which he has been preparing for many years, but has not found time to complete. The reason for the delay is that he has been sorely distracted by the large number of sick nobles committed to his charge, and by the grievous weakness of his

own small body, which makes him incapable of long hours of labour. The complete work was never published, but the brief letter must have been considered of unusual importance, since it was reprinted several times,[1] and enjoyed a life of over a hundred and twenty years. The abstractors of the Royal Society, however, writing in 1809, considered the letter of such slight interest that they did not reprint it. Schrader in 1674 asserts that Joseph was the first to claim that the embryo is present in the egg before incubation, and much later, in 1752, Parsons mentions that according to Joseph the chicken is already formed in the unincubated egg in the same manner as the plant is present in the seed before germination. The reference to preformation in Joseph's letter is very brief. He only says that the chick is fashioned in the egg before it is incubated by the hen, and afterwards grows as the result of the maternal heat and the nutrient material in the egg, assisted by those vital principles derived from the atmosphere. Joseph accepts generation *ex ovo*, but rejects spontaneous generation. Such was the simple beginning of an hypothesis which was to hang like a millstone round the neck of the embryologist for over a century.

Sir Kenelm Digby (1644), in a short paragraph, refers to a preformation doctrine 'held by some', according to which 'the embryon is actually formed in the seed, though in such little parts as it cannot be discerned until each part have inlarged, and increased itself, by drawing into it from the circumstant bodies more substance of their own nature'. Harvey, however, following Aristotle, holds that 'there is no part of the future foetus, actually in it [the egg], but yet all the parts of it are in it potentially'. In another place he mentions foetuses 'in quibus forma oritur ex potentia materiae praeexistentis'.[2] In these passages we have the first application of the term pre-existence to an embryonic state, and also the first hint of a *molecular* preformation in the egg,

[1] In the *Phil. Trans.* reprint it is stated that the letter was first published at Frankfurt in the year 1625. This is an error, the Frankfurt edition bearing the date 1626

[2] *De Generatione*, 1651, p. 122.

which is variously accepted by modern embryologists. Highmore's work on generation, published in 1651 some two months after Harvey's, which Haller refers to as a 'work almost unknown', expounds a theory of generation which halts between pangenesis and preformation. Highmore appears to have been the first observer to study the development of an animal 'by the help of a microscope'. Malpighi usually enjoys the credit of this. Harvey in three places mentions using a perspicil or perspective (magnifying glass). The seminal atoms, says Highmore, are already in their proper places in the cicatricula [blastoderm] of the egg, and have the same relative disposition as in the older and visible embryo. Even in the cicatricula before incubation there is some distinction of parts, which never vanishes with development, but becomes still more distinct. 'So that these seminal Atomes as soon as they are conjoined in a convenient place, by the due ordering and regulating of the specifick soul, put themselves in order, fall to their proper places, and make up a Chick before the Egg be perfected.' This is a form of preformation, without emboîtement, vaguely expressed and doubtless vaguely conceived, but important as indicating the trend of contemporary thought.

In an early criticism of Harvey by Ross (1652), who declares that Harvey's views on generation are as offensive to others as they are to himself, the embryo is derived from the male seed, in which alone the formative faculty is said to reside, the female having only a passive role, and producing no active seed. Having apparently forgotten this statement, Ross proceeds to criticize epigenesis in the following words: 'The egge is not altogether a body inorganicall actually, seeing it hath different parts. Besides, it is organicall potentially, as containing in it all the parts and members of the chick that shall bee. So the seed of other animals contains potentially the animal that shall be, with all its members; therefore the common opinion is, that seed is drawn from all parts of the body because it contains in it all the parts.' Ross's attitude favoursa type of speculative preformation very similar to that supported by Highmore. It is

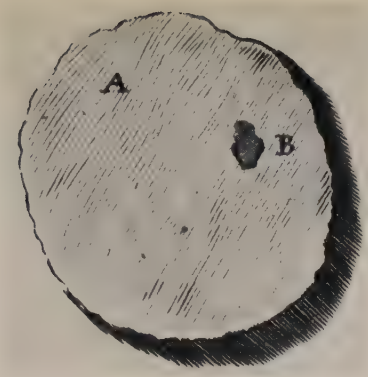
Fig. 6. Illustrating Swammerdam's analysis of the life history of a butterfly. IV, Caterpillar about to undergo metamorphosis, from which, after treatment with hot water, the butterfly shown at A and B can be extracted. V, the chrysalis—a later stage than A and B and differing apparently from it, but nevertheless a butterfly, as shown when its parts are displayed as in C. E, the mature chrysalis about to liberate the perfect insect. F, the empty chrysalis case in four parts after the escape of the butterfly. D, G, H, the escaped imago expanding to form the perfect insect shown at VI. From these facts Swammerdam concludes that the butterfly was in the caterpillar, or in other words, the caterpillar *is* the butterfly and hence there is no epigenesis

difficult, however, to reconcile the two passages which have just been quoted, unless by egg he means the fecund egg, and even then we are left wondering what his opinions actually were. Power, another early microscopist (1664), is also disposed to discredit epigenesis, and to lean towards preformation. He states that as soon as the pulsating particle appears in the chick, the microscope most distinctly shows it to be the *complete* heart with both auricles and ventricles, and not having one auricle only as supposed by Harvey, and, furthermore, the auricles can be observed to pulsate before the ventricles. 'So admirable is every organ of this machine of ours formed, that every part within us is intirely made, when the whole organ seems too little to have any parts at all.' He believes the heart and circulation to exist even in the second day chick, but that they are not discernible owing to the fact that the circulating liquid is white and not yet converted by heat into red blood. On this latter point Malpighi later expressed similar views. Finally Descartes (1664) seems to have held that the first animal and the first man included the elements or rudiments of all their posterity, but, as Fontanelle observes, 'it is necessary to admire Descartes always and to follow him sometimes'.

Thus the doctrine of preformation, inherited as a faint outline from medieval philosophy and Church dogma, was in the air, and only required the addition of some fragment of observation to precipitate it as a tangible and attractive hypothesis. The man to achieve this dubious success was Swammerdam. In his first work on Insects, published in 1669, he refers to, but does not quote, the passage in Hebrews vii. 9–10, in which Levi is represented, not only as receiving tithes, but as having paid them, long before he was born, through Abraham, inasmuch as he was in the loins of his father when Abraham was paying tithes to Melchizedek. This passage was understood by Swammerdam to express a belief in preformation, which it can only do on the assumption that the 'father' referred to pre-existed in the loins of Abraham. Swammerdam himself had just discovered that the larva of the butterfly was present in the egg, and in its

turn enclosed anticipations of the pupa and imago. The four stages therefore, egg, larva, pupa, imago, were enclosed in that order as in a series of diminishing boxes, and he was consequently beguiled into the belief that generation was not, as it appeared, a series of recurring epigenetic cycles, but an unbroken and continuous process involving the successive emergence, and development by growth, of a series of individuals which had been simultaneously brought into existence at the creation of the world. Later, in the *Biblia Naturae*, he says: 'The beetle is only a nymph disengaged from its skin, and changed by accretion; as the nymph likewise is only a worm that has changed its skin, and is altered or transformed in the same manner: hence these several states exhibit only one insect under three different appearances.' Swammerdam severely criticizes Harvey for his statement that the insect pupa is an egg, and he adds that Harvey's dissertation contains almost as many errors as words. According to Swammerdam the egg encloses the larva, the larva the pupa, and the pupa the imago, but although these stages are described as overlapping, he does not go so far as to claim that they all exist simultaneously, or that the imago *as such* is present in the egg. He implies, however, that it is represented by some mystical simulacrum which produces the imago by expansion and accretion, and he is therefore neither a strict preformationist nor an epigenesist, but his attitude could only develop logically in the direction of preformation and encasement (emboîtement). On this view alone, he claims, can we understand how a man deprived of hands and feet nevertheless produces complete offspring, and the question is settled whether a concentration of seminal particles from all parts of the body is necessary to produce a perfect foetus. Also, in the opinion of a 'learned friend', we can explain biologically the burden of original sin, for all mankind was represented in the loins of the first parents.

A few years later, in 1672, in the first edition of his work on the structure of the uterus, Swammerdam restates and somewhat modifies his position, and in a later edition of the



a

b

Fig. 7. *a*. Human ovum three or four days after it had reached the uterus. After Kerckring. Head and body differentiated, with traces of the sense organs, but no perceptible limbs

b. Human ovum a fortnight after conception. Shows placenta, with umbilical cord, and homunculus, with face and principal parts of the body developed

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same work he discloses the fact that the 'learned friend' is Malebranche. He now boldly affirms that the whole human race was comprehended in the loins of Adam and Eve, and consequently the race will be faced with extinction when this original supply of germs is exhausted. Thus death, the penalty of sin, is implicit in the human race. It is evident that Swammerdam does not allow his mind to be disturbed by any considerations of consistency. Reasoning from his own observations he should be an ovist—the foetus is preformed in the egg, and the male parent has no direct share in it. And yet he finds a use for Adam in generation, and appeals to St. Paul for confirmation.[1] The belief that the male parent supplies the seed and the female the soil, and that by the co-operation of these diverse elements the foetus is produced, is of great antiquity, and is strongly entrenched in Hebrew tradition. It is this view that St. Paul is endeavouring to illustrate in his epistle to the Hebrews, viz., that descent is through the male sex. Hence, when the Jew is concerned with questions of inheritance, we encounter such expressions as the 'seed of *Abraham*', and it is the iniquity of the *fathers* that is visited upon the children. It is strange that Swammerdam did not realize the implications of his own opinions, especially as he was familiar with Harvey's dissertation, the kernel of which was the famous dictum *ex ovo omnia*. De Launay, writing in 1726, refers to the inconsistency, but himself interprets the Levi passage as implying that the male seed produces males and the female seed females, since if the female parent produced males and females indifferently, Levi would not have descended from Abraham but directly from his mother.

In the *Miraculum Naturae* Swammerdam states that the black portion of the frog's egg is a little frog complete in all its parts, and that the white part of the egg is only the food of the embryo. 'It is the more wonderful that this same little frog appears already in the ovary and has the beginning of its growth, but withal so small as almost to evade the

[1] The reference to Adam and Eve is included in an edited Latin edition of the *History of Insects* published in 1693, but is omitted in the *Biblia Naturae* of 1737.

sight. Yet the animal itself is hidden under this minute fundament.' In the *Biblia Naturae*, however, beyond the bare statement that the foetus of the frog is in the egg before it leaves the body of the parent, there is no mention of preformation in the section on the frog. From these observations, and also from his work on Insects completed before 1669, Swammerdam draws the conclusion that there is no real generation in Nature, but only a growth and development of pre-existent parts, since all the parts of the foetus are contained in the egg. An incident mentioned by Boerhaave is relevant in this connexion. In 1661[1] Thevenot entertained a convention of learned men at his house in Paris. Swammerdam was present, and the generation of animals came up for discussion. He was asked for his opinion, but, being no orator, he preferred to explain the matter by a demonstration rather than by reasoning. At the next meeting, therefore, he produced a silkworm, and the company having failed to find in it any trace of a moth, he removed the skin, and exposed the wings, proboscis, antennae, and appendages of the future moth, from which it followed that these parts had been a long time formed before they were unfolded and brought to view. The same idea was adopted and extended to the human ovum by Kerckring (1671), of whose work Haller says: 'parvus libellus, sed maximi momenti, si fidem ei dare liceret.' In an ovum three or at most four days old, Kerckring professes to have found the rudiments of a child having a head and body. The head bore indications of its principal parts, but the body was as yet undifferentiated. A later ovum of fifteen days had a head provided with eyes, nose, mouth and ears, and a body with legs and arms. Man therefore arose *ex ovo*. 'Who would have believed,' he says, 'had the knife of the anatomist not disclosed it, that the cradle of man no less than of birds was to be found in the egg.' The validity of such a contention depends on the identity of the early eggs in the uterus with those in the ovary, but Kerckring does not profess to carry this point beyond the region of probability. Kerckring's

[1] In the *Biblia Naturae* the date is given by Swammerdam himself as 1668.

results were suspected—especially the existence of the foetus in the early human ovum. He was also accused of plagiarism and even of serious crimes.

On March 14th, 1671, Croone deposited with the Royal Society the manuscript of a paper on the development of the chick, a brief abstract of which was published in 1672, but the complete paper in Latin appeared much later, in 1757.[1] Croone affirms that his work was written a good while before, and he is therefore definitely anterior to Malpighi. After referring to Harvey in terms of the utmost respect,[2] he proceeds to describe how he 'made an observation of the greatest import in this matter which completely escaped so careful an inquirer into Nature as Harvey'. Croone started by examining eggs which had just been laid, and had therefore not undergone incubation. 'I had even summoned to my aid a skilfully contrived microscope (which chanced then to be at hand), yet I perceived that I was gaining no advantage, and that by its aid nothing was presented to my eyes which I could not see without it, although somewhat small in form.[3] I for my part, to tell the truth, would be over willing to have seen anything which could confirm my previously conceived opinion concerning the instantaneous generation of living creatures, and their birth by means of metamorphosis, as the expression is.' Having made up his mind what he wanted to see he now proceeds to see it, or as he himself puts it, 'I suspected that at some time or other something would be found in the egg which would give every one a confident belief in the truth of this opinion.' Nevertheless he met with so little encouragement in his early experiments that when at last the critical egg was in his hands he had almost abandoned his first opinion. This egg was obtained immediately after laying, and had therefore

[1] The original Latin MS. of this communication does not exist, but there is a fair copy of it by an amanuensis in the archives of the Royal Society.

[2] 'I am unwilling to appear so zealous an inquirer after truth as to be guilty of a shameful act [i.e. criticism] against a man who in all ages is worthy of memory, and to whom I ought to gaze up in awe from a distance.'

[3] Later in the paper Croone mentions the microscope again, this time with more appreciation.

not been incubated by the hen. It was placed near the fire for a short time after the cicatricula (blastoderm) had been exposed and the white drained away. He next dissected off the cicatricula and subjacent yolk, and threw them into a dish of warm water, whereupon a

'membrane like a very faint mist separated from the yolk and this floated while the yolk sank . . . I noticed that this membrane swarmed with well nigh innumerable little filaments like small veins'.

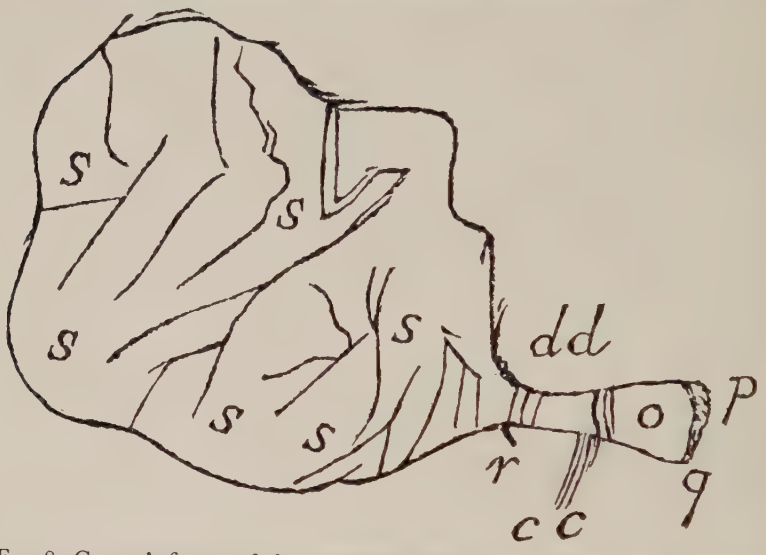


Fig. 8. Croone's figure of the preformed chick. *s*, the membrane [vitelline membrane]; *o*, *p*, the two bosses [eyes]; *q*, the beak; *dd*, the milky ribs; *r*, the rudiment of the foot; *cc*, the umbilical vessels

Later there seemed to be lying hidden underneath it

'some thick matter which bore down by its own weight the extremely slender and delicate little membrane. . . . As I watched this matter more intently I seemed to see something very like the head of an embryo or chick. This I had absolutely no difficulty in recognizing. . . . Next I scanned with eager eyes all there was to see, and observed quite clearly and distinctly those two rather large bosses which are the eyes, with the beak lying in between. I saw besides little ribs of a milky colour, and the rudiments of feet just showing. There extended from the stomach as it were two filaments, fairly strong, with jagged ends,

as if they had been wrenched off from somewhere . . . these were the umbilical vessels. . . . For my part I could not but congratulate myself that I chanced to be the first to see the chick in the egg—I do not say before the appearance of Harvey's punctum saliens [heart], but even before the hen had sat on it at all. . . . Harvey certainly declares that the egg is prepared for the embryo stage after the first four days of incubation; he little saw that this embryo already previously existed in the egg hidden beneath the cicatricula. . . . Nowhere do any signs or proofs of a future chick appear without the whole chick being already present at the same time. . . . I think it nearer the truth that the whole question is decided once and for all at the moment of conception. . . . It is clearly manifest that the heart cannot produce repeated contractions without the help of brain and nerves, and so by this reasoning too it could be established that the brain must necessarily be in existence as often as the beat of the heart is noticed, even if this belief is not confirmed by observation. But experiments so far afford no certainty as to the precise moment when the chick is first seen, since in eggs of a better strain this happens before any kind of incubation by the hen, and perhaps before the egg is laid. . . . From the observations which I have duly carried out we must return to the opinion according to which the chick is produced complete at one stroke as it were endowed with all its parts, at the very moment of conception,' the opinion of Harvey to the contrary notwithstanding. 'So much for this my first, indeed my main, and, if I may say so, my fundamental observation.'

Croone's paper is important not on account of its merits, which are negligible, but because it is the first reasoned attempt, based on observation and illustration, to establish the corporeal existence of a preformed foetus in the unincubated egg. It should be noted that Croone does not concern himself with encasement or emboîtement, and has no explanation to offer of the origin of his foetus beyond that it probably materialized quite suddenly. The modern zoologist will not fail to detect at a glance where Croone went astray—it is sufficiently obvious that his foetus is nothing more than a fragment of the vitelline membrane, which has accidentally caricatured the features of a bird. The very size of it should have warned him of his error, and he cannot have paused to reflect how such a preformed chick could possibly be transformed into the well-known embryo of the fourth day.

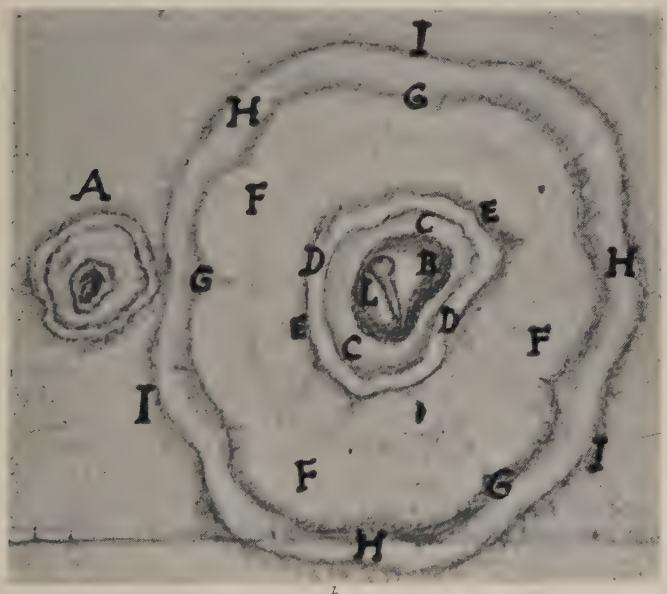
In 1672 Le Grand translated the passage in Swammerdam quoted from St. Paul, and it is interesting that he should refer in detail to this speculation without identifying it as a preformation hypothesis. Swammerdam, however, does not label it as such himself, and it is significant that he was not understood as supporting a theory of pre-existence by at least some of his contemporaries. In his important work on the development of the rabbit, published in 1672, in which it was established that the Vivipara proceed from eggs no less than the Ovipara, de Graaf attaches first importance in generation to the egg, and hence favours the ovist convention.[1] He is not, however, a preformationist—in fact, so far as his own work is concerned, he finds no trace of the foetus in the early 'ovum' of the rabbit. It does not, he says, appear as a definitely recognizable embryo before the tenth day, and this in an animal whose period of gestation is only thirty-one days. The substance, whatever it is, discharged from the ovary only assumes a *visible* vesicular form after it reaches the uterus, and it is then called an ovum.[2] 'What are found in the ovary must not be regarded as perfect ova, but as the primordia or rudiments of them.' He noticed that the early uterine egg was in point of size ten times less that the ovarian 'egg', and although this would suggest that he distinguished between the true ovum and the Graafian follicle, there is no evidence that he ever saw the free ovum itself. It is obvious that there is here no suggestion or even hint of the existence of an organized body in the ovum, however defined such a body may be.

Malpighi occupies a unique position in the history of the preformation doctrine—the position of a man who could see one thing and believe another. Few men are capable of faithful observation in the face of strong preconceived opinions, and when these two interests are in conflict we know only too well which of them is sacrificed. In Malpighi

[1] Several authors in 1672, such as Swammerdam, Malpighi, Croone, and Kerckring, favoured an *ex ovo* hypothesis in Frogs, Birds, and Mammals respectively.

[2] The term 'ovum' was first applied to the ovarian follicles of Mammals by van Horne in his *Prodromus* of 1668. Harvey's use of the word is discussed elsewhere.

a



b

FIG. 9. Malpighi's figures of the preformed foetus in the chick—in *a* at C, D and in *b* at L, B. Photographed from the original drawings in the possession of the Royal Society

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we have a notable exception to this tale of surrender. His observations are sound to the smallest detail, in spite of the fact that his theoretical views are flatly opposed to them. And in this we detect a failing of a different, but less ignoble, type—in which contending interests are kept apart, and are not permitted to react on each other to the advantage of truth. The cicatricula of the egg, says Malpighi, is large in impregnated but small in unimpregnated eggs. The embryo is visible in a bubble in the centre of the *fertilized* but *unincubated* cicatrix, lying within a very thin and transparent amnion. The head, spine, and associated structures are easily seen. These parts pre-exist in the egg, and precede incubation, in the same way as the seeds of plants contain the essential parts in miniature from which the plant develops. He concludes that the head with its brain, the spinal cord, and other parts with their tunicles or coats are present in the cicatrix of the fowl's egg before the embryo moves or develops red blood, and *before the egg is laid*. This differs from Harvey, who found no clear traces of the embryo before the third day. In the unfertilized cicatrix, however, *no traces of the foetus were found*. Malpighi's actual words, which have become famous, are as follows: 'Quare *pulli stamina* in ovo *praeexistere*, altioremque originem nacta esse fateri convenit, haud dispari ritu, ac in Plantarum ovis.'[1] It is true that Malpighi describes the development of the embryo as happening gradually, but he does not believe that the parts are formed gradually. The heart, for example, does not *beat* until 38 or 40 hours after incubation, but it *existed* before. His reasoning on this point may be summarized in the following words: At the 36th hour the region of the umbilicus is covered with small vessels forming a complete network. In this network, however, there appear to be gaps both large and small. But these gaps cannot be real, and the network there is only invisible because it lacks the red blood content. Therefore the entire plexus is perhaps present in the cicatrix, but only becomes visible by the flow and movement of the red blood as it penetrates into it during the

[1] 1673, p. 4.

growth of the foetus. Malpighi believes that all the parts are formed at once by a kind of precipitation, after, and as the result of, fertilization, but they are so small that they only become perceptible, even under the best microscopes, as they are successively unfolded and grow. He is therefore a preformationist, but is by implication definitely opposed to emboîtement. It has been suggested, and the suggestion is a reasonable one, that his error in discovering a developed embryo in an apparently unincubated egg was due to the egg having undergone artificial incubation in the heat of the sun of an Italian summer.

It was inevitable that encasement or emboîtement,[1] the logical consequence of preformation, should at the outset be grafted on to the parent fiction. This conception of an endless series of embryos, each of which was encasing and encased like a nest of boxes, was first developed in detail in 1674 by the philosopher Malebranche, to whose influence its acceptance over a long period may be directly traced. The idea, however, had occurred to several of the Greeks and the Fathers of the Church, and is vaguely suggested in the spurious Hippocratic treatise *De Diaeta*. That Malebranche in his turn was only developing material which he had obtained from Swammerdam is undoubted, and Hartsoeker tells us that he also communicated the results of his observations on the spermatozoa to Malebranche. The line of argument followed by the philosopher is characteristic. Since, he says, the animals of microscopic life move like others, they must have legs and feet, skeleton, muscles, tendons, and blood system. We must assume this because these animals live, feed, and move voluntarily from place to place. 'The imagination is lost and astonished at the sight of so strange a smallness', but 'our sight is very limited and it should not limit its object', and in this small world are found as many things, although smaller in proportion, as occur in the larger world in which we live. Perhaps these small animals have others which parasitize them, which may be imperceptible on account of their incredible smallness. What

[1] German, *Einschachtelungstheorie*.

a mite is to us these animals will be to a mite. Malebranche then discusses the divisibility of matter, and considers it possible that there may be a series of animals becoming smaller and smaller to infinity, although our imagination may be scared at the thought. If, however, animals exist a thousand times smaller than a mite, why should we suppose that they are the last and smallest of all? It is on the contrary more reasonable to believe that there are animals much smaller than any which have been discovered. He next proceeds to consider the structure of the bulb of the tulip, and comes to the conclusion that the germ of the bulb encloses a complete tulip, from which it is reasonable to assume that a grain of mustard seed or the pip of an apple contains each a complete plant of its kind, although it cannot be seen with the eye, or even with the microscope, and one may claim with confidence that all trees exist in miniature in the germ of their seed.

Having committed himself to this treacherous slope the reasoner soon proceeds to move with accelerated velocity. It even appears, he says, not unreasonable to conclude that there are an *infinite* number of trees in a single germ, since it may contain not only the tree of which it is the seed, but also a very large number of other seeds, which may all enclose in themselves further trees and further seeds of trees, which latter again may enclose in an incomprehensible smallness other trees and other seeds as fecund as the first, and so on to infinity. Such a thought only appears extravagant and fantastic to those who measure the wonders of the infinite power of God by the dictates of their senses and imagination. He assumes further, as Bonnet did after him, that the member of the series whose turn it is to mature is not the only one to grow, but that all other members at the same time grow in proportion to their position in the series, and in this way slowly prepare for hatching.

Malebranche applies the same view to animals, quoting Malpighi on the chick and Swammerdam on the frog, which authors, he says, have discovered that the embryo is preformed in the egg of the hen and the frog, and he expects

the same discovery will be extended to other animals when they are examined with the necessary skill and experience. But, he adds, it is not necessary that the mind should wait for the eye, for the vision of the soul is indeed more comprehensive than that of the body. The bodies of all animals which have ever been born are perhaps the products of the creation of the world, and the females of the first animals were probably stocked in the beginning with all those generations which have ever been developed or ever will be to the end of the world. One might, he concludes, push this speculation even further and perhaps with much reason and truth, but one rightly dreads to penetrate too deeply into the smallest works of God.

IV

DEVELOPMENT OF THE PREFORMATION DOCTRINE

FROM about 1674 the Preformation Doctrine was generally accepted, and it was only a question whether the miniature was in the egg or in the sperm (Ovism and Animalculism). Epigenesis, which had never been popular, or even seriously considered, was for the moment dead. At first the Ovists were without rivals, but the discovery of an analogue to the egg in the form of the spermatozoon favoured for a time the Animalculist version. Animalculism, however, definitely expired after almost a century of existence, the Ovist convention having predeceased it, but the renewed interest in Epigenesis which had in the meantime developed was at first checked by the revival of Ovism, due to the work of Haller, Bonnet, and Spallanzani. During the whole period of the Ovist and Animalculist controversy little research was carried out—in fact the continuance of the dispute depended directly on the absence of a microscopic investigation of the early stages of development. So long as naturalists were content to apply the methods of abstract disputation to a problem which could only be resolved by the microscope, this amazing dispute was bound to continue. The contribution made in 1680 by Perrault, the most distinguished member of the Parisian school of Comparative Anatomy, illustrates this point. He emphasizes our ignorance of the essential processes of generation. To attempt a new hypothesis, he says, is like marching on a dark night along an unknown road. Nevertheless he makes the attempt, and it is one which seeks to explain the generative function both in animals and plants. He is an Ovist and a Preformationist. The function of the male is to transform and vivify generally the vital processes of the female. A formative and subtle ferment is thus engendered, which penetrates into the ultramicroscopic vessels of the foetus, causing them to enlarge and assimilate nourishment, and consequently to develop and expand. The miniature foetus is only a potential organism,

which before this metabolic transformation is a 'little animal not yet alive'. These miniatures were all created together, and have existed since the beginning of the world. Generation therefore consists of two distinct processes: (1) the production by the female under the influence of the male of the ethereal ferment, which reacts on the dormant and miniature foetus and prepares it for expansion; (2) the generative process proper, or the nutrition and development of the animated foetus. On metamorphosis Perrault adopts the views of Swammerdam, although he does not quote him. In the metamorphosis of an insect there are no parts formed anew as appears at first sight—wings and appendages have been there from the first but have lacked size and visibility. He admits that on his hypothesis it is difficult to explain the resemblance of offspring to their parents, but submits that it is still more difficult to do so on the principle of epigenesis. This makes it necessary to fall back on supplementary theories, such as the imagination of the mother and the 'movements of diverse humours'.

We may now deal with the whole of Leeuwenhoek's contributions to the early history of the embryo, which date from 1683. He was, as we should expect, an Animalculist—in fact he was the first to direct attention to the importance of the spermatozoa or seminal animalcula in animal development. He believes that they impregnate the eggs, but that the embryo does not come from the egg, which is concerned only with the nourishment and growth of the foetus arising from the animalcule. In support of this he quotes a case of Mendelian dominance in rabbits, in which the male colour only reappeared in the progeny, which latter were in fact so like the wild male parent that they were sold as wild rabbits. Such a result, he says, is manifestly a case of generation *ex animalculo*, and this letter, dated July 13th, 1683, is very important as indicating the parts which he supposed the egg and sperm to play respectively in generation. Two years later Leeuwenhoek adds the detail that in the uterus the spermatozoon casts off its tail, and the head then becomes the foetus. In fertilization the sperm does not lose its dis-

tinctive character as an organism, and is only influenced by the egg in so far as the latter acts as a nidus for it. He now concedes sexual differences to the sperms, and his mind is inclining definitely towards the preformation hypothesis. He examined a very small foetus of a sheep and found that it possessed all the parts of a sheep, and he argues that if this be so in so small a foetus there is no reason why one even smaller, such as the seminal animalcule, should not possess a set of organs, although their existence cannot be established by observation. He refers to the *Collectanea medico-physica*,[1] in which it is stated, on the authority of C. Bontekoe, that Leeuwenhoek believed the sperm of man and animals to be full of small children and foetuses according to their kind. Leeuwenhoek denies this, and points out that insect larvae are not insects although insects proceed from them, and, likewise, spermatozoa are not children although children proceed from them. His attitude, however, is by no means consistent, and he is apparently finding it difficult to accept a philosophical speculation which does not admit of proof by microscopical observation.

In 1699 Leeuwenhoek had before him the letter of Dalenpatius, whose figures he reproduces, in which spermatozoa are illustrated as having the structure of little men. In commenting on this letter Leeuwenhoek wrongly accuses Dalenpatius of ascribing a blood system and circulation to the spermatozoa,[2] and he is certain that the Royal Society will not accept the seminal homunculus. He will not admit that the frog's egg contains a young frog, but the parts of the embryo appear gradually in the fertilized egg, nor does the embryo when it does appear resemble a frog. Nevertheless the frog must be locked up in the fertilized egg, but he does not say that it is locked up in the form of a miniature frog. He says he has examined the seed of a man a hundred times, and has never seen anything like the figures of Dalenpatius, and holds that they are entirely fanciful and imaginary. One

[1] By S. Blankaart, 1683.

[2] This is strictly not Leeuwenhoek's mistake, but that of a Dutch medical friend who translated the Dalenpatius letter for him.

of his criticisms is subtle and to the point. The foetus of the Vivipara in the uterus, he observes, is always curved, and even the limbs of the new-born infant are not extended, whereas the spermatic homunculus of Dalenpatius is represented as being perfectly straight.[1] He admits that the substance of the human body must be included in the seminal animalcule, but he cannot conceive it possible that a definite human shape will ever be seen in it microscopically. He refutes the assertion of Dalenpatius that some sperms are of larger size (i. e. those containing the foetuses), and dwells on the ease with which errors of observation can be made in microscopic work, which must explain how the mistake had arisen. Only a portion of the original manuscript of this letter by Leeuwenhoek, which bears the date of June 9th, 1699, still exists in the archives of the Royal Society, and there are no figures to it. As, however, the latter would be copied direct from the plate which illustrated the letter by Dalenpatius, they would naturally be wanting. Owing to an engraver's error, these figures, in the collected editions of Leeuwenhoek's works, are invariably bound up with the wrong letter, and are understood by many writers,[2] who have not taken the precaution to consult the text, to be Leeuwenhoek's figures, and to represent his own conception of the spermatozoa. The result has been that Leeuwenhoek is generally, but quite wrongly, credited with having described homunculi in spermatozoa. Nevertheless Leeuwenhoek was unquestionably a philosophical preformationist, and even hints at emboîtement. In two letters written in the same year, he remarks that when we consider how great a secret is locked up in the seed of the apple, may we not assume that an entire man is locked up in the animalcule of the male seed, and that these animalcules all take their origin from the first man? He overcomes the difficulty of size by referring to other and well-known microscopic organisms, which in spite of their small magnitude must yet possess complex parts. But, he concludes, the study of the minute structure of the spermatic

[1] Buffon also stresses this objection.

[2] Even the scholarly Miall fell into this trap.

animalcule is beyond human knowledge, and we stand amazed at, and cannot comprehend, a minuteness which is outside microscopic vision.

Further reflection only confirms Leeuwenhoek's belief in an intangible preformation. In 1701, after criticizing Hartsoeker's seminal homunculus, he asserts that every spermatic animalcule of the ram contains a lamb, but it does not assume the external appearance of a lamb until it has been nourished and grown in the uterus of the female. He compares such a development with the life history of a fly, in which the earlier stages include the later, although they are not externally visible. If this were not so the transformation of the fly would be inconceivable, and hence we must assume a corresponding complexity in the spermatic animalcule. He calls upon the reader to marvel that the tail of so minute an animal should be composed of joints, muscles, and blood-vessels, but he is careful to add that they are so small that it is impossible to observe them. In 1722, however, he produces definite evidence in support of preformation in the shape of an embryo sheep of a supposed age of less than five days. In this specimen he described the vertebrae of the neck and back and also the joints of its short tail, and he thought he saw the eyes also. He cut the foetus into fifteen slices, and concluded that it had intestines, bladder, heart, brain, and blood-vessels. That a uterine foetus of not quite five days old, he says, should possess all these structures disproves the statement that at the beginning of its development it is nothing but an unformed mass. The obvious comment on this passage is that the foetus could not have been of the age stated by Leeuwenhoek. In his final pronouncement on the spermatozoa, published in 1724 after his death, Leeuwenhoek refers to several criticisms of his opinions on generation, and especially to the revival of the Ovist point of view which was occurring at that time, some authors even denying the existence of the seminal animalcula. He stands by his own descriptions, repeating that he has found animalcula in the semen of all types of animal life.

Brunner (1683), in a criticism of Peyer, argues against

preformation on the ground that if the parts of animals are preformed in the egg, withal so small as to escape observation, it is impossible to explain the production of monsters which appear from time to time. Such productions represent a deviation from the normal course of development, which can only originate in the uterus. It is generally believed, he says, that monsters are the direct result of

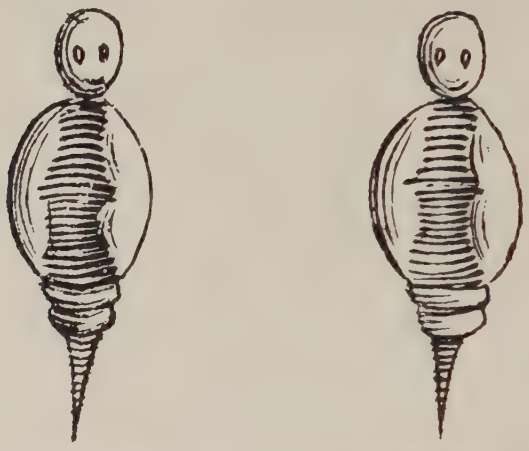

Fig. 10. Cestode parasites exhibiting the homuncular form, after Redi

the mental state of the pregnant woman, but how can such an influence affect a foetus whose form has already been determined?

It would be superfluous to take account of the observations of the arch-plagiarist Snape, in spite of his repeated assertion that they are 'wholly his own'. His timidity in acknowledging the sources of his information is exemplified by his reference to the 'saying of some old philosophers, *ex ovo omnia*, that all things are from an egg'. If we eliminate the pirated extracts from de Graaf and Harvey, the residue will represent what he has taken from minor authors.

In 1684 the distinguished naturalist and poet Redi figures two parasites from the gut of a female octopus, which are interesting as illustrating the tendency to detect the human form in the smaller animals—a tendency which was respon-

sible for the seminal homunculi of later authors. Redi says that the flesh of the belly and 'the stomach was studded all over the outside with tubercules, and each tubercle enclosed a little very white and living worm'.[1]

The long and somewhat monotonous chorus staged by the supporters of preformation is relieved by the humorous criticisms of Drelincourt (1685). According to Blumenbach, 'Boerhaave's teacher Drelincourt collected from the writings of his predecessors no less than 262 groundless hypotheses on generation, and nothing is more certain than that his own system made the 263rd.' In the English translation the last part of the sentence is mercifully omitted. How Blumenbach made the number up to 262 is a mystery, unless he accepted the estimate of a contemporary reviewer of Drelincourt's work, in which an identical figure is given,[2] and even if it is based on the whole of Drelincourt's works the total is excessive. Launois,[3] in professing to quote Drelincourt, who applied to each author he criticized a derisive epithet intended to ridicule his particular blunder, writes as follows: 'He [Drelincourt] names the anatomist Fernel, who believed in the mixture of the two seminal liquors, *Fernelius seminator*. Plazoni, who assumes a fermentation similar to that of flour to which leaven has been added, becomes *Plazoni pistor*, i. e. baker. Barbatus, who supposes that the menstrual blood plays the principal part in fecundation, is labelled *Barbatus liquefactor atque fusor*. As for van Horne, according to whom the mixture of the two seminal liquors produces a species of marmalade, he is called *Casearius*'. If Launois' transcription be compared with the passage in Eloy,[4] of which it is a plagiarized version, and this in turn with Drelincourt's original

[1] Mr. Dobell, who encountered these parasites during his work on *Aggregata*, informs me that they are the larval Cestodes known as *Scolex polymorphus*. According to Southwell several species are included under this name.

[2] 'It would take too long to discuss all the fables which Drelincourt has refuted both on the subject of children who were born in their membranes, and on other matters of which he has treated in his work *De Conceptione*. One may count as many as 262 items in which he has claimed to have refuted error.' *Nouv. Rep. Lettres*, 1685, pp. 803–4. Prof. Punnett drew my attention to this passage.

[3] *Les Pères de la Biologie*, Paris, 1904.

[4] *Dictionnaire historique de la Médecine*, t. ii, p. 93, 1778.

text of 1685, the growth of fiction will receive a not unpleasing illustration.

Drelincourt's own theory of generation was never fully developed. He believes that the egg will not germinate until it has been impregnated by the male semen. The egg is enveloped in strongly porous tunics, and the most subtle parts of the male semen enter the egg on all sides by these pores. As the seminal atoms are very active, it is certain that they enter the egg very impetuously, but nevertheless without confusion. They then proceed to occupy their appointed stations in an orderly manner, and in this way they produce the first rudiments and organs of the foetus. It thus follows that the active and material principle of the embryo comes solely from the male. He implies, but does not definitely assert, that the ovum on the other hand is already furnished with the chorion, amnion, and the rudiments of the placenta whilst still in the ovary, and hence all these parts are derived from the female parent. The foetus makes use of the substance of the ovum as its first aliment. Drelincourt therefore is an animalculist, but hardly a preformationist, since he assumes that the foetus is formed more or less suddenly as the result of fertilization, and does not preexist in the sperm. It is surprising that he should devote so much attention to the speculations of his predecessors and yet ignore the Preformation hypothesis—the most popular if not the most important of them all.

The well-known comparative anatomist Peyer devotes some attention in 1685 to the occurrence of monsters, which are obviously inconsistent with a Preformation doctrine. He is unable to explain them except on the ground that they are either the result of the imagination of the mother, or of the machinations of the Devil, the foetus being deformed in the uterus as a punishment for sin. He declines, however, to attach any importance to monstrosities, which cannot affect the order of Nature, and from which no general conclusions should be drawn. He therefore abides by his conviction that the plan of the foetus is laid down and preexists in the egg, but in a plastic form, and it may thus be

defaced or transformed during the period of uterine development. An anonymous writer in 1687 argues against Malpighi's belief in the sudden precipitation of the foetus following fertilization, holding that it is impossible to understand how a complex organism can arise from undifferentiated matter in that way, except by the special intervention of an infinitely intelligent cause. It is, he says, much simpler to believe that the unbounded power of God produced all the germs at the beginning of the world, so that nothing was left for Nature to do subsequently but to stimulate the growth of these latent organisms. This criticism was commonly expressed at the time, and voices not so much a repugnance to epigenesis, as a general belief that the world was wound up at the beginning like a clock, and then left to run down by itself.

Boyle (1690) takes his opinions on generation from Malpighi and Harvey without apparently realizing that they were not compatible, but the Scottish divine Garden (1691) works out a philosophical system of his own. He believes that the egg is essential to development, though not responsible for the form of the embryo. He uses the familiar type of argument. Complexity of form can be established by the microscope however far back the embryo is traced, and hence it is probable that it still characterizes even the ultramicroscopic stages.

'An animal is not the sudden product of a fluid or colliquamentum, but does much rather proceed from an animalcule of the same kind, and has all its little members folded up according to their several joints and plicatures, which are afterwards enlarged and distended. . . . It seems most probable, that the stamina of all the plants and animals that have been, or ever shall be in the world, have been formed, *ab origine mundi*, by the Almighty Creator within the first of each respective kind. And he who considers the nature of vision, that it does not give us the true magnitude, but the proportion of things; and that what seems to our naked eye but a point, may truly be made up of as many parts as seem to us to be in the whole visible world, will not think this an absurd or impossible thing.'

He then proceeds to argue that the foetus is in the sperm and

not in the egg, maintaining that the form of the sperm as disclosed by Leeuwenhoek agrees with Malpighi's description of the rudiments of the foetus both before and after incubation. Since the foetus only appears in the egg after fecundation by the male, it must therefore be derived from the sperm, the ovum only supplying it with the proper nutriment. In further proof that the foetus is not preformed in the egg, he points out that the unfertilized egg, when incubated, decomposes, but that the fertilized egg on the contrary develops and produces an embryo.

The first investigator of the structure of bone, Clopton Havers (1691), regards generation as 'one of the great secrets of Nature which our senses cannot observe or art imitate'. He apparently accepts preformation, or at all events considers it a defensible hypothesis, but makes use of humours, fermentations, spirituous vapours, and volatile particles in the production of the foetus. This collection of simulacra is presided over by the heart, which controls the development of the foetus as a whole. He is, however, not unconscious of the medieval character of his suggestions, for he adds that he passes from 'these conjectures to the consideration of that subject [the bones] . . . which does in many things offer itself to our senses, and encourages us with fairer promises of certainty and satisfaction'.

Ray, in a careful discussion of the rival theories of generation (1693), concludes that each organism possesses from the beginning all the eggs it will subsequently bring forth, and that when they are exhausted it becomes barren. If, he argues, the individual has the power of producing eggs at any time, why are so many present at first? He quotes the philosophers as assuming that the first pair of a species when created must have been endowed with ovaries and testes, and hence not only that generation but also the next was provided for at the same time. But the second generation also from its first appearance must have had its clusters of eggs, each with a foetus in it, which therefore must have been created simultaneously with its forebears. The same may be postulated for succeeding generations—in fact for all genera-

tions that shall exist to the end of the world. Ray's objection to this speculation, which, however, he does not press, is the purely physical one that the ovaries of one female could not contain the innumerable myriads which would proceed from it during the life of the world. Such an assumption involves an inconceivable and almost an infinite divisibility of matter. On the other hand it is possible that the foetus may be formed out of prepared matter, and not from a minute animalcule in the seed. He sums up finally in favour of the pre-existence of the foetus in the egg, and the creation of all generations at the beginning, but he prefers to approve this as a conjecture and not as an established doctrine. This brings him to the 'new opinion of Mr. Leeuwenhoek that all animals proceed from an insect or animalcule in the male sperm', which he rejects 'because of the necessary loss of an incredible multitude of them which seems not agreeable to the wisdom and providence of Nature'. If, however, the foetus is in the egg, such a loss does not occur, since the number of eggs is proportioned to the various needs of the animal, and they 'may, if need be, be all brought forth, and come to perfection'.

The first author to figure a foetus locked up in the seminal animalcule is Hartsoeker, but until his *Essay de Dioptrique* was published in 1694 he had never even hinted at such a possibility. He now thinks that in Birds each animalcule encloses a male or female bird of its own species. In referring to the homunculus which he figures he says that *if* we could see the little animal through the skin which hides it we *might* possibly see it as it is represented in the illustration, except that the head perhaps would be greater in proportion to the rest of the body than is shown in the drawing.[1] He does not therefore claim that the figure is based on anything more than supposition. Blumenbach's comment on this effort of the imagination is characteristic. He refers to the figure of the 'lynx-eyed' Hartsoeker as a 'little embryo sitting in the

[1] Hartsoeker's work was reviewed in the *Journal des Sçavans* for Feb. 7th, 1695, and the figure of the homunculus was reproduced, but not printed from the same block.

body of each animalcule in the same crooked and confined posture as in the female womb . . . and which appeared to him as if anxiously expecting its deliverance'. Hartsoeker proceeds to add that this new view of generation may be pushed much further, and we may claim that each of the male animalcula encloses within itself an infinity of other animals of the same species *male and female*, but infinitely small. Hence the first created males enclosed all those of the same species which could ever be engendered to the end of time. The theory is also applied to plants. This of course is emboîtement, and it is specially interesting because Hartsoeker is the first author to assume that the members of a series enclosed, for example, in any one animalcule are not all *of the same sex*. This important point will be discussed later. It is Hartsoeker's specific contribution to the doctrine of encasement. In his later publications, however, he completely abandons his earlier views. At first he is silent on the question of emboîtement, but in the end he criticizes it in severe and contemptuous terms. In 1708 he describes the spermatozoa of Birds and Mammals. There is no mention of a foetus in them, and he states that a foetus some days old would not possess arms and legs but only warts representing those appendages. By 1722 Hartsoeker has definitely abandoned preformation in any form, and his reason for doing so was a consideration of the facts of

Fig. 11. Human spermatozoon with included homunculus, after Hartsoeker

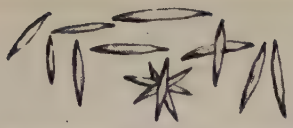

Fig. 1. *Trabeculæ aut partes salis fluctuantes in semine.*

Fig. 2. *Animalium unum innatans.*

Fig. 3. *Animal alterum exuto* Ζύφῳ *membris integris apparens.*

Fig. 4.
Eadem quæ 3ª sed hac major.

FIG. 12. Figures of the crystals of spermine phosphate and of homunculi in the male human semen, after Dalenpatius

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regeneration. The intelligence which can reproduce the lost claw of a crayfish, he says, can reproduce an entire animal. He is the first to recognize that the phenomena of regeneration are inconsistent with preformation, and the criticism that epigenesis involves an act of creation with each generation is shown to be without point, since a regenerated limb *is* essentially a new creation. Having thus been induced to abandon preformation, Hartsoeker is thrown back on an Intelligence, or whatever it may be, which resides in an animal, and is responsible for the replacement of lost parts and the production, in the appropriate laboratories of the body, of the spermatic animals, which he still believes are responsible for the foetus. In his work of 1722 Hartsoeker appears to have been the first after Andry (1714) to use the word emboîter. He says: 'Dans le commencement Dieu a créé en raccourci, & emboité, les uns dans les autres, tous les arbres, toutes les plantes, & tous les animaux qui ont déja été produits, & qui le seront dans tous les siécles à venir, & qu'ainsi tout n'est qu'un développement continuel.' This, he adds, is a view too hard to digest.

Hartsoeker, in his work published posthumously in 1730, replies to Leeuwenhoek's criticisms of his homunculus of 1694 in the following words: 'Il [Leeuwenhoek] parle contre la figure de ces animaux que j'ai fait graver dans mon Essai de Dioptrique, & il a raison, quoique cela ne soit dans le fond qu'une chicane. Le Graveur a fait la queuë de l'animal trop mince vers le corps, & trop égale par tout. Il n'y a pas, dit-il, de tels animaux dans le Monde; mais il se trompe, puisqu'on en trouve dans de l'eau croupie, qui ont une queuë très-longue & comme un filet'. It is not easy to determine how much is admitted in this ambiguous passage, but it is significant that Hartsoeker makes no serious attempt to defend his seminal homunculus. However this may be, there is no doubt as to his final views on preformation. This doctrine, he says, is so absurd that he cannot understand how it could be entertained by a man of sense. If all the animals of any species had been enclosed in the first male or female, as supposed by Swammerdam, Malebranche, and many others, those which now inhabit the earth must have

been at the time of the Creation of a smallness truly infinite and incomprehensible. If, for example, all the rabbits which have been produced since the beginning had been enclosed in the first male rabbit, a rabbit existing to-day would have been at the time of the Creation, not as unity is to unity followed by 60 zeros, which is about as a grain of sand is to the whole earth, but as unity is to unity followed by more than 100,000 zeros. To reach this truly appalling result he assumes that a seminal animalcule of the male rabbit is at least ten thousand million times smaller than the rabbit itself, that the creation of the first rabbit took place about six thousand years ago, and that rabbits begin to reproduce at the age of six months. Again, preformation does not explain the existence of monstrosities, such as polydactylism, the presence of only one kidney, and the reversal of the viscera, i.e. where organs which occur normally on the right side are displaced to the left, and vice versa. Nor can preformation explain the regeneration of lost parts, such as the limbs of the crayfish and the feathers of birds, which can be plucked out a hundred times and renewed each time exactly as before. Finally, on the preformation hypothesis all things would be predetermined and inevitable, and nothing open to adjustment. Therefore since the creation of the world God could only have been a passive spectator of the expansion of works which had cost Him but a single initial effort. Hartsoeker also remarks that Leeuwenhoek, in his 116th letter, had refuted very fully and with much futile and unnecessary language one named 'Daleparius', who had claimed to have discovered a little animal in the semen of man. But, says Hartsoeker, this could have been refuted in three words. It was only necessary to point out that even an embryo of three or four weeks is nothing but a large head, and that no limbs can be distinguished. In saying this Hartsoeker is ignoring his own spectacular homunculus of 1694.

Leibnitz (1695), following Swammerdam, Malpighi, and Leeuwenhoek, 'the most distinguished observers of the time', favoured the preformation system, and concluded that there

was no such thing as generation as usually understood, but only expansion of an already organized nucleus. No animal therefore comes into existence when we think it does, and preformation holds both in the material and the spiritual worlds. The souls and the bodies of men have always existed in a miniature state, and are thus independent of conception. In various letters to Bourguet (1714–15), written shortly before his death, Leibnitz is unable to decide finally between the ovist and animalculist versions of preformation, and neither, he admits, accounts for the influence of both parents in generation. Finally he inclines towards animalculism as the more plausible of the two, and pleads for a respectful consideration of Leeuwenhoek's views. Leibnitz was not an observer, and never claimed to have examined microscopic organisms or germs himself—an honest admission which earned for him the commendation of Voltaire. On the other hand Locke attacks pre-existence in his controversy with Bishop Stillingfleet (1697), and examined the theory in some detail. The Bishop supported preformation because it was implied by the Christian doctrine of Special Creation and the Resurrection of the *same* body. Such a dogma postulates the successive maturation in this world of individuals specifically created at the beginning, and continuity with the next world through the resurrection of the same body. Locke attacks pre-existence as here defined in a somewhat involved passage, and announces his inability to conceive that all the wheat in the world is but one grain, which would indicate that, although he quotes Leeuwenhoek, he had not sufficiently instructed himself in the preformation doctrine, since its difficulties are not so much those of conception as of verification. The Bishop asserted that the little organism of the seed is the 'same body with that which it grows up to', since the presence of 'organical parts' had been proved microscopically in the seed by 'most accurate observations'. Locke's objection to this is that he cannot understand how a body may be increased in bulk a hundred or a thousand times and yet continue the same body. This he could only believe when

he had 'learned to say that a part and the whole are the same'.

Dionis (1698) is an ovist, and considers that this theory is one of the chief benefits which the discoveries of anatomy have given to his age. 'The foetus is certainly lodged in an egg, but the manner of its formation there is a great difficulty which remains to be adjusted.' He is not prepared to accept Swammerdam's emboîtement hypothesis, which, however, 'although almost incomprehensible, is not necessarily ridiculous'.

In 1699 Plantade, writing under the name of Dalenpatius,[1] described and figured homunculi in the male semen, and a translation of this notorious letter is now appended:

'Extract of a letter from M. Dalenpatius to the promoter of these Nouvelles, containing a curious discovery made by means of the microscope.

If philosophers in their attempts to discover the causes of natural phenomena would make diligent inquiry of Mother Nature herself, they could not possibly give birth to such monstrous fictions as they daily produce. Personally I have ever held this opinion, and have made it a principle to utilize every means at my disposal, so that if any way of approach to Nature should open, I might examine it with great care, and strive by all means in my power to reach her innermost secrets. At last one such way, and that a most certain one, has happily brought success beyond my hopes. With my microscope—than which I believe (if I may say it without boastfulness) hardly any better could be made, since the lens is little bigger than a dot which can only just be seen[2]—I was diligently examining the constituents of human semen, and first of all (mark you) I observed a certain aqueous substance, whose parts could in no way be discriminated.

[1] Plantade's pseudonym has been variously spelt by authors who were evidently not familiar with the original letter, the worst offender in this respect being Good (1807), who refers to him as 'Delappius, a pupil [? follower] of Leeuwenhoek'. He was not a pupil of Leeuwenhoek, although this statement is frequently made—in fact there is no evidence that Leeuwenhoek ever saw him.

[2] This refers to the fact, well known at the time, that the smallest biconvex lenses had the highest magnifying power.

Floating in this liquid were a number of small rigid staves of different sizes, but for the most part about a third of a line thick and two lines long, and pointed at both ends. These little spars, as they might be called, either drift about alone or attach themselves to one another, and so entangled and interlaced they rather remind one of a sea urchin, or those caltrops which are thrown down before an attacking force to stop the advance of cavalry. When a number of them have collected together, and lack moisture, they cohere to form clumps, which those who first examined semen, using inadequate microscopes, have declared to be a kind of hair. I am of the opinion that these bodies are really particles of salt, and I am firmly convinced that the pleasurable excitation at the time of coition arises from their friction. In addition I detected certain animalcules, of almost the same shape as the young of frogs which are seen in the month of May in streams and muddy swamps. Their bodies scarcely exceed in size a grain of corn, though some are rather larger, whilst their tails are four or five times the length of their bodies. They move with extraordinary agility, and by the lashings of their tails they produce and agitate the wavelets in which they swim. Who would have believed that in them was a human body? But I have seen this thing with my own eyes. For while I was examining them all with care one appeared which was larger than the others, and sloughed off the skin in which it had been enclosed, and clearly revealed, free from covering, both its shins, its legs, its breast, and two arms, whilst the cast skin, when pulled further up, enveloped the head after the manner of a cowl. It was impossible to distinguish sexual characters on account of its small size, and it died in the act of uncovering itself. This metamorphosis, though unheard of before, should nevertheless not seem strange, seeing that many other animalcules daily put on new forms. Perhaps indeed it was this fact which gave rise long ago to the idea of metempsychosis. I next observed the constituents of the blood, which I found to be solid translucent spherical bodies half a line in diameter, floating in the same

medium as that of the semen—which medium perhaps acts as a vehicle for all the humours of the body. These particles settle and coagulate when the serum evaporates. I shall publish shortly a dissertation, perhaps neither useless nor uninteresting, intermingled with various observations, on the particles which generate the venereal disease, arthritis, and other disorders, subjects not hitherto treated except by conjecture; and therewith many other things concerning the circulation and nourishment of the sap in plants. Meanwhile I wished to publish these things that the learned might make known what they think about this matter. Diagrams are attached.'

The fact that this letter was published simultaneously in Amsterdam, London, and Edinburgh, seems to imply that it was an organized and serious attempt to deceive the public.[1] Plantade was travelling in England and Holland in 1699, and when in the latter country he became friendly with Bayle, who was associated with one of the journals in which the letter appeared. The identity of Dalenpatius was first disclosed by Astruc in the third edition of his work on the venereal disease published in 1740.[2] In his early years Astruc was closely connected with Montpellier, where Plantade was born and lived, and he established friendly relations with Plantade. Astruc says that Plantade was a man of genius who, when he was young, was given to jesting, and composed the letter to amuse himself. He published it under the name of Dalenpatius, which is an anagram based on the Latin form of his name—Plantadeius.[3] He might, adds Astruc, have been pardoned for writing the letter, had he not given it out that he had actually observed the homunculus with an excellent microscope, and deliberately

[1] The figures in these three versions are all different, but engraved from the same original.

[2] Bourdon mentions Dalenpatius under his real name of Plantade, and so also does Gleichen (1778), who refers to Plantade's witticism, and states that he confessed to it. Czermak (1833) lists the letter under Delampatius and T. Planta de (*sic*), without stating that they are the same person.

[3] According to Ehrenberg, Plantade first converted his name to Dalenpat and then added the Latin termination.

invented figures to support his statements. On this account Astruc condemns him as the 'false and fallacious Dalenpatius'.

Although the letter was not accepted at the time, it was debated quite seriously by Leeuwenhoek, Vallisneri (1721), Buffon (1749), Bourdon (1830), and others. Buffon believes that Dalenpatius described what he thought he saw, but that he was deceived. The notion, he says, is 'repugnant to the repeated experience and observation of all those who have hitherto made inquiries into this subject'. His main objection is that according to Dalenpatius the human form is more completely developed in the spermatic worm than it is in the uterus of the mother at the end of the fourth and fifth weeks. This he considers to be an unanswerable objection. Even Haller (1774), who was acquainted with the identity of Dalenpatius, does not question his veracity, but allows that he saw what he wanted to see. Later, in 1778, Haller observes that Dalenpatius was not indeed an impostor in spite of this lapse—referring perhaps to the fact that in later life he was devoted to serious pursuits, and established for himself a respectable reputation. Cloquet (1827), however, who also knew Dalenpatius as Plantade, refers to him as a practical joker, who had been accepted as a bona fide observer by Buffon and Vallisneri. Plantade, he says, amused himself at the expense of credulous observers, many of whom were deceived by the jest.

The dramatic moulting of the homunculus staged by Dalenpatius is frequently referred to by other writers,[1] and was doubtless inspired by Swammerdam's famous experiments on the metamorphosis of insects. It was assumed at the time that during development the parts of most animals increased in size and acquired firmness under a skin or 'robe de chambre', which was cast off when the process was completed.

In one respect Dalenpatius does not go beyond what can actually be seen. He describes and figures quite accurately

[1] Blumenbach, for example, says: 'Dalenpatius actually saw one indignantly burst its wormy skin and issue forth a perfectly formed human being.'

the crystals of spermine phosphate, *which occur only in human semen*, and were first mentioned and crudely illustrated by Leeuwenhoek in 1679. Dalenpatius' figures are, however, undoubtedly original, and it seems certain therefore that he did examine human semen under the microscope. This gives an air of verisimilitude to the letter, and increases the difficulty of settling how much of it represents genuine research. Did he see the spermatozoa at all? His Figure 2 would indicate that he did, if it were not for the dimensions which are given. The animalcules [spermatozoa], he says, 'scarcely exceed in size a grain of corn,' and could therefore have been examined without a microscope. His over-estimate of the size of the crystals ($\frac{1}{6}'' \times \frac{1}{36}''$) is not inconsistent with his having seen them, and is not sufficiently inaccurate to favour the suggestion that his comparison of a spermatozoon with a grain of corn represents *apparent* size under the microscope. The only conclusion that can be drawn from these facts is that Dalenpatius saw the crystals, but invented the rest. Whether his letter was a satire on current beliefs, and intended to cover animalculism with ridicule, or whether he was ambitious of appearing as a great discoverer like Leeuwenhoek, can only be conjectured.

The helminthologist Andry, who saw worms everywhere and in all diseases, and was consequently labelled by Vallisneri the *Homo vermiculosus*, is naturally an animalculist, and names the spermatozoon the Vermifoetus. At first he regards the spermatic worms as 'probably' useful, and identical with the foetus. In man, he says, they have much larger heads than in other animals, which agrees with the proportionately larger head of the human foetus. The worms, which perhaps are either male or female, are the epitome of the animals which are to be developed from them. They enter the egg in the uterus, grow into foetuses, and then burst the membranes of the egg and are born. When they become foetuses the tails disappear, just as the tails of tadpoles vanish when they take the form of frogs. We must, however, not conclude from this, he says, that the semen of dogs contains little dogs, that of cocks little pullets, and of

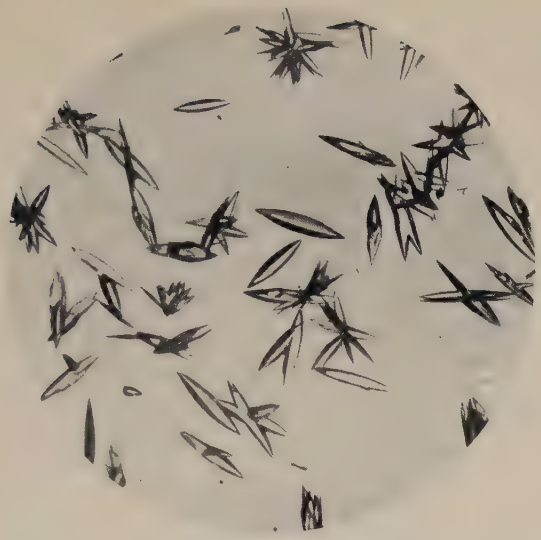

Fig. 13. Photomicrograph of the crystals of spermine phosphate from human semen, after Rosenheim (1924)

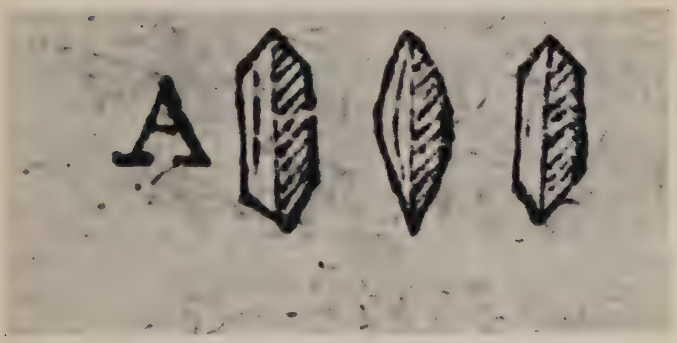

Fig. 14. Leeuwenhoek's figures of the crystals of spermine phosphate

men little children. Nevertheless, and here he is by no means consistent, the spermatic worm has all the organs and tissues of the adult animal, and lacks only the external form. Later his opinions become more decided, and he accepts emboîtement in the male and the creation of all generations at the beginning of the world. 'Nature does nothing but develop these small organized bodies. She produces a sensible growth in the individuals which have emerged from the germ, and an invisible growth, but none the less real, *and proportional to their size*,[1] in those which are still enclosed in the germ.'

Andry is the first author to use the term *emboëter*. In his second edition of 1714, this word is substituted for *abréger* in the following expressions: 'Des animaux emboëtés les uns dans les autres'; 'ces germes emboëtés'; 'les vers spermatiques emboëtés soient plus petits que ceux qui les emboëtent'. His attempt to explain the intermediate character of hybrids was subsequently adopted and extended by Haller. Andry says that when the horse is paired with the ass, the progeny, on the emboîtement theory, should resemble the father, since the form is determined by the male sex. The actual result, as is well known, is an intermediate, which has points in common with both parents. His explanation of this is that the juices which the spermatic worm of the horse encounters in the uterus of the ass, being adapted to produce a greater development of the ears than the juices which the same spermatic worm would have found in the uterus of one of its own species, it follows that the ears of the foetus will respond by a more vigorous growth. But the ears of the horse are not capable of *all* the growth to which such a nourishment is adapted, and therefore we should expect them to be longer than those of the horse, but shorter than those of the ass. In other words, they are *de facto* the shorter ears of the male parent hypertrophied by the stimulus they have received in the uterus of the female parent. Such an explanation, he adds, may be applied to all anomalies which arise as the result of pairing animals of

[1] This important qualification, which was to be worked out in detail by Bonnet, does not appear in the third edition.

different species. This addition to the emboîtement theory was not convincing even at the time, since it involved the assumption of particles of nourishment which produce a specific effect, and it was a matter of common observation that a single species may flourish on a variety of nourishment, whereas dissimilar species may sustain a great diversity of form upon the same nourishment.

Emboîtement, whether in egg or sperm, was attacked by Tauvry in 1700. This theory, he says, may have the advantage of simplicity, but it is contrary to the laws of Nature, in the works of which nothing is wasted. When therefore we are asked to believe that in order to produce a man it is necessary to sacrifice many millions of germs, he is unable to acquiesce. Moreover, the seminal animalcula have no significance in generation, since organisms may be discovered by the microscope in vinegar, rain water, common water, and in almost all liquids. Geoffroy and Du Cerf (1704), however, are animalculists, and accept emboîtement in the first man. Generation in any animal or plant is not the production of a new being, but the development of a very ancient one. 'Deus creavit omnia simul.' The non-fecundated egg contains no part of the foetus, but is merely the place where one of the spermatic animalcula is received and nurtured. Only after fecundation does one perceive in the cicatricula of the egg a little animal (the spermatic worm), which develops and acquires the figure of its species. In a later letter, which was not published until 1741, Geoffroy asserts that the assumption of the ovarists that the germ is in the egg is gratuitous, and since one cannot by any device see it in the egg before fertilization, although it can be easily discovered afterwards, it is much more natural to believe that the foetus is not preformed in the egg, but that it arrives at the moment of fecundation. If one examines the cicatricula of the egg at that moment one finds there the spermatic animalcule in the form of a worm. It begins to grow and unfold immediately, and is no longer recognizable as a worm, but undergoes the developmental changes of the species of animal to which it belongs.

In 1704 fresh evidence in support of preformation in the

egg was produced by Littre. At that time the French Academy, with the exception of Méry, accepted the generation of man by eggs. Méry argued strongly and at length against it, and Littre was put up to remove his objections. He professes to have discovered in the human ovary an egg which put the ovist theory beyond dispute. It contained a foetus which was a line and a half broad ($\frac{1}{8}''$) and three lines long ($\frac{1}{4}''$). This foetus was attached to the membranes of the egg by an umbilical cord, which was one-third of a line thick ($\frac{1}{36}''$) and more than a line and a half long ($\frac{1}{8}''$). It had a head with a small mouth, a nose, indications of eyelids, and a trunk with rudiments of fore and hind limbs, the first named being the smaller. This, he says, was all he was able to distinguish with the assistance of a lens. A microscope was not used. In criticizing this paper, Buffon remarks that such a foetus was never seen by any eyes but the author's, and it was only necessary to read the paper to be convinced of its dubiety. The account, he says, is given in a 'very suspicious manner'. Bourdon (1830) proclaims also that Littre's observations are evidently false. Nevertheless, in spite of these unfavourable opinions, it seems probable that Littre was describing a case of ovarian pregnancy, which is now well known to occur. An earlier case was published by de St. Maurice in 1683.[1] This was claimed to be the first description of such an occurrence, and was hailed as supporting the doctrine of the 'formation of the foetus in the testicles of women and consequently of the existence of eggs'. It is obvious that Littre's case, if accepted, could not fail to be regarded as a striking confirmation of the doctrine of preformation in the egg. Méry, however, was not convinced, although he admitted that the 'system of the generation of man by eggs is to-day very commonly accepted'.

Passing over the work of King (1705), who advocated a form of philosophical emboîtement 'by most men assented unto and by very few denied', and who attempted to expound the rationale of the Universe without a specific knowledge of any part of it, we find Bellefontaine (1712) support-

[1] *Phil. Trans.* 13, p. 285.

ing preformation in the spermatic vermiculus, and an anonymous writer (1714) rejecting it both in the egg and sperm. The latter does so on the evidence of hybrids and grafts. A disbelief in preformation, he says, 'is at this time universal'. It has never been proved, but only deduced from the analogy of the seed of plants, in some of which the young plant has been discovered by the microscope. Goelicke (1717) attacks the theory of generation *ex animalculo*, which, he says, is an ingenious but laughable proposal to be the favourite fiction of a Leeuwenhoek. He then proceeds to criticize the theory with no small degree of rancour, but not with much reason. If, he says, these tailed vermiculi are little embryos, why do they not produce a tailed foetus? Again, and with more reason, if the rudimentary foetus resides only in the male semen the sterility of females is left unexplained. These and many other objections are vehemently urged against the 'monstrous conception of Leeuwenhoek'. Another instance of the tendency to discover the human form in small animals, of which an example from Redi has already been examined, is to be found in the work of Joblot (1718). The organism in question was found in an infusion of 'anémone', and it is drawn natural size (= 3 cm. long without the tail). The back is covered by a mask having impressed on it a complete representation of the human face. What is this animal? Its dimensions (if given correctly) rule out the ordinary aquatic species, but it is at least probable that the statement on this point refers to *apparent* size under the microscope. If this be so the animal may well be a larval Hydrachnid, with its anterior sucker and three pairs of legs. Some species exhibit a dorsal pattern which might be converted into a caricature of the human countenance.[1] As Ehrenberg points out, such markings have no more significance than the death's head on the thorax of a well-known moth, and Joblot's interpretation is nothing but a trick of the imagination—the sport of a weak and casual observer.

Bradley (1721) is an animalculist but not the complete preformationist. In the unfertilized egg there is not the

[1] Since this was written Oudemans has reached a similar conclusion.

least trace of an animal, and any assertion to the contrary is a 'bare supposition', which the best microscopes fail to confirm. The embryo, however, comes into existence suddenly in the egg at the 'very instant of fecundation'. The seminal

Fig. 15. Homunculus in an aquatic animal, after Joblot

animalcules are the 'principles of generation or the beginning of man and other animals'. They vary in structure according to the species in which they are found. Bradley compares them with the larvae of insects, and they produce the adult by a similar type of metamorphosis. This metamorphosis, however, supervenes immediately after they have entered the eggs, when they begin to take on their specific form. Adam must have 'had in himself all the animalcules, as it were, encased one within the other'. All animals were created at one time, and therefore we need not 'torment

ourselves to find out how organized bodies may form themselves', since there is nothing to study but the unfolding and demonstration of their parts one after another in the seminal animalcule. This view, he says, 'is the more general and has less suppositions than the others'. It is significant that Bradley's version of preformation shows some approximation towards epigenesis. There is no miniature in the egg, and only a dubious one in the sperm, the foetus becoming visible as such only after fecundation.

In the very elaborate treatise on generation published in 1721 by Vallisneri, a pupil of Malpighi, we find a lengthy refutation of Leeuwenhoek and the *ex animalculo* theory. Nor is he in entire agreement with its *ex ovo* rival, and he even denies that the Mammalian ovum is known, since it is too delicate and transparent to be perceptible. He reproduces the figures of 'Dalempazio', whom he accepts as a genuine worker, but regards the figures as the offspring of a visionary and an indifferent observer, who made the facts fit in with his speculations. Vallisneri favours the position taken up by Swammerdam and de Graaf, and accepts emboîtement. In the original mother of mankind all future generations were imprisoned, but although the foetus pre-exists it only becomes visible during development.

Maître-Jan in 1722 traces the growth of the chick from the twelfth hour of incubation to the time of hatching, and also includes some notes on the anatomy of the newly-hatched animal. He rejects the animalculist theory on grounds such as the following—among others which are too trifling to be mentioned: The spermatic worm of a bird, for example, cannot be a miniature of the adult, for it could not swim in the seminal liquid without having the organization of a fish or at least of a frog, and how does it throw off its fish-like characters when it enters the egg and begins to take on the form of a bird? If his opponents object that a foetus which which is not fish-like can live and be nourished whilst still in the amniotic liquid, he replies that this is only possible because of a reciprocal exchange of blood between the mother and the foetus or the yolk and the chick, whereas the

spermatic worm is independent and free living in the seminal liquor. Maître-Jan's observations on preformation are more important. He holds that the external and internal membranes of the yolk are continuous with the peritoneum and membrane of the gut respectively, and that the same system of blood-vessels is common both to the foetus and the yolk. Further, the yolk membrane becomes part of the chick when it is hatched. From this it follows: (1) that the yolk membrane is continuous with that small white body [cicatricula] in the unfecundated egg which is really the commencement of the chick, or in other words the chick itself in an imperfect state; and (2) that the yolk membrane is enormously extended merely to enclose the substance of the yolk (which latter serves to nourish the chick before it hatches), and to transmit the vessels which convey this nourishment to the embryo. Hence the small white body or miniature chick with its membranes were already formed when the egg was in the ovary, and they can in fact be seen in the smallest ovarian eggs before the yolk is deposited. Therefore the substance of the embryo is derived from the egg and has no relation to the cock, the latter supplying only the leaven and fermenting spirit which sets development in motion the moment the egg is incubated. Maître-Jan is consequently an ovist and a preformationist, but not to the extent of recognizing a complete miniature in the egg. It should be noted that the passage which has just been summarized is a remarkable anticipation of Haller's defence of preformation of 1758.[1]

The system of generation published by De Launay in 1698, and reissued with additions in 1726, favours the view, at that time becoming popular, that the foetus in miniature becomes visible suddenly at the moment of conception or immediately after. De Launay is opposed both to the ovists and animalculists, his own system assuming that in man the semen of each parent contains a small foetus of its own sex, one of which survives as the result of complicated manœuvres

[1] The debt is more or less admitted by Haller in his *Bibliotheca Anatomica*, ii, p. 15, where he says also 'melius est opus quam vulgo creditur'.

in the uterus which are not easy to comprehend. It is doubtful, however, whether this author ever made a single original observation on the development of either a mammal or a bird, and his book consists of lengthy disputations, without figures, based on what he has read. Volpini (1726) is an ovist and a preformationist, and so also presumably is an anonymous writer of 1727. The latter, who refers to himself as a medical man, after stating that many distinguished observers flatly deny the existence of the seminal animalcula, develops a view of his own which has at all events the pleasing aspect of novelty. He admits the existence of the animalcula, but believes that they are polymorphic and identical with those seen in water under different shapes. In generation they penetrate the ovum, get into the rudiment of the embryo, are shut up in its vessels and mix with its fluids, circulate with the blood and juices, live, and lay their eggs and breed in the body of the foetus. He thus regards the seminal animalcula as intrusive organisms, but whether they contain the beginnings of a human foetus, or whether each is an entire and perfect man, as Leeuwenhoek is said to believe, he does not decide, but defers the inquiry to another opportunity. Bourguet (1729) is another ovist and preformationist. He admits the existence of the seminal vermiculi, which, he says, exercise a stimulating effect on the 'small organized machine' in the egg, and by mixing with the contents of the egg influence the development of the foetus, and thus explain the intermediate character of hybrids. He disputes Hartsoeker's calculations, the object of which was to reduce the theory of emboîtement to an absurdity, and as the result of his revision he concludes that the egg which was created in the first year of the world would be to the last and smallest to appear at the time of writing as 630,720,000 is to 1. This, comments the eager and flamboyant Bonnet, is very small compared with the terrifying mathematics of Hartsoeker.

It is a relief to pass from these crude speculations to the clear and informative reasoning of a Réaumur. In the first volume of his great work on the *History of Insects* (1734) he

emphasizes the importance of Swammerdam's discovery that the butterfly is not a new formation, but can be traced through the pupa into the larva. It is well known how brilliantly this discovery was exploited by Réaumur himself. On the old view, he says, the metamorphosis of insects was regarded as a kind of resurrection. The transformation of the chrysalis into the butterfly was supposed to give us a picture of one of the greatest mysteries of our religion—the resurrection of the body. This interpretation, however, must now be abandoned. We can, by the dissection of the *larva*, discover the butterfly under its skin, and it is not even necessary to wait for the moment of transformation. All the parts are there, albeit more folded and contracted and otherwise arranged than in the pupa. Moreover, these parts may always be found, and are not present merely at the onset of metamorphosis, and their discovery in larvae even very small is perhaps only a question of greater dexterity. Malpighi found eggs in a pupa two or three days old, but Réaumur finds them in larvae some time before metamorphosis. These eggs were very small, but quite recognizable. Such facts incline Réaumur to the preformation doctrine, the outlines of which he gives, but he is only willing to adopt it tentatively, until such time as the early stages of development can be accurately studied in detail. It is only then that it will be possible to discriminate between preformation and epigenesis. In the meantime, in the absence of definite proof that an animal is 'created' at every generation (i.e. is formed by epigenesis), we must assume, he says, that development is only a matter of growth and enlargement of a preformed miniature. In a later work (1749) Réaumur describes an attractive theory of pangenesis, and promises the publication of his own researches on genetics.

Morgan (1735) is an animalculist who even goes the length of working out the period of gestation in man by comparing the bulk of the spermatozoon, representing the initial form of the foetus, with the foetus at birth. This he does by calculating the time it would take the foetus to bridge the gap between these two stages by regular growth. 'That all

generation', he says, 'is from an animalculum, pre-existing *in semine maris*, is so evident in fact, and so well confirmed by experience and observation, that I know now of no learned men, who in the least doubt of it.' Gesner (1737) also strongly favours animalculism. Pre-existence, he observes, refers all the glory of generation to the Creator at the beginning, whereas epigenesis relies on chance or a fortuitous concourse of particles—a cause which could never produce the body of an animal. He denies, however, that the homunculus has been seen in the sperm, and points out that Leeuwenhoek never found anything more than a head and a tail. Nevertheless *reason* compels us to believe that an entire man in miniature is enclosed in the little spermatic worm. Such a belief is expressed also by the microscopist Baker (1742), who accepts the complex structure of the spermatozoa, the tails of which must have joints, muscles, nerves, arteries, and veins.

The celebrated insect anatomist Lyonet (1742) opposes Leeuwenhoek and Andry on the spermatic animacules. He declines to discuss ovism, which he 'leaves to its own fate'. The system of Leeuwenhoek, he says, is built on no solid foundation, but is a mere conjecture whose only merit is some slight degree of probability. He quotes with approval a statement by Swammerdam that in some insects,[1] which possess spermatic worms, the foetus is formed in the egg before fecundation, and therefore without the assistance of the male. Assuming that the foetus develops from an animalcule, he is staggered by its rate of growth. In the bitch it would have grown to five hundred million times its original size in ten days, and if they grow so rapidly in the uterus, why do they not grow in the semen of the male which is their native medium? He is deeply impressed, as were so many others during the period of this controversy, by the incredible destruction of animalcules on Leeuwenhoek's theory, which destruction does not correspond with what occurs in the operations of Nature, where wastage has no place. To the answer that there is a similar wastage in

[1] He means the frog.

the seeds of plants, he replies that seeds are used for other purposes than generation, e.g. the nourishment of animals, whereas the excess of spermatic animalcula is an actual wastage. If the animalcula represent human foetuses they must be provided with a rational soul, and 'can we conceive that, in order to form our body, the least noble part of our being, God was willing to create so many hundreds of millions of rational souls only to destroy them'. If Andry had considered this fact, he says, and the consequences which flow from it, rather than support the system of Leeuwenhoek, the pen would have fallen from his hand and that part of his work would never have been written. Lyonet therefore rejects the animalculist theory as being destitute of all proof, full of difficulties, contrary to probability, and subversive of the ideas we should entertain of the perfection of the divine majesty. In reply to a letter from Le Cat in 1764, Lyonet observes that Swammerdam in more than one place in his works asserts that the foetus of insects lives and is endowed with feeling and movement in the egg *before fecundation*. This is a misquotation, but it would be correct if the last two words were omitted. Moreover the passage does not mean, as Lyonet seems to imply, that the foetus is *preformed* in the egg, but that it can be detected in the egg before hatching. In discussing emboîtement, Lyonet, adopting the statistical method of Hartsoeker, rejects it as a physical absurdity. He concludes that he is not enough of a philosopher to accept without proof a hypothesis which so startles the imagination, and only a philosopher would be prepared to find germs anywhere—even in places where the Devil himself would not think of looking for them.

In 1743 one of the pupils of Astruc, who had attended his course in 1740, published an English translation of his lecture notes, of which no French version can be traced. It is, therefore, necessary to bear in mind that the extraordinary opinions attributed to Astruc are based on the record of a student.[1] Astruc is said to favour animalculism, the spermatozoon being responsible for the foetus, and the

[1] Astruc's own version, as published later, is not widely different.

egg for the placenta and membranes—a belief common enough at the time. If, however, the foetus is derived solely from the male parent, how are the resemblances to the female parent to be explained? It is on this point that Astruc is credited with convictions which are not only novel but bizarre. As the sperm 'introduces itself into the pore or passage of the ovum, it is therein shaped, and, as it were, moulded; whence it is more or less stamped to the likeness of its mother, whose lineaments are impressed by the author of Nature on the hole or passage through which the animal enters the ovum'. If it is a tight fit, the maternal features are the more deeply impressed on the sperm, but if a loose one, less so. Hence the varying degrees of resemblance to the mother. The female sperm is said to be larger than the male, and therefore undergoes greater moulding to the maternal type. This explains why daughters tend to duplicate the mother, and sons the father. In the treatise of 1765, published by Astruc himself, the latter statement is reversed, and the male sperm now figures as the larger, so that boys conform to the mother and the girls to the father. By varying the size and contour of the pore, the mode of inheritance of any parental characters may be readily explained.

Boerhaave (1744) is not a convinced animalculist, but he believes that *probably* the seminal animalcula contain the future rudiments or foundation of the whole body, in which case they must also possess its organs. When they are 'received into a fit place or nidus, and there supplied with most subtle nourishment, forwarded by a friendly warmth and motion, they grow up and unfold themselves, so as to display the latent parts of which they are composed even to the naked eye'. He admits that these animalcula live where the external air has no access, and that he is quite ignorant of their exact origin. Every animal, even man, is hence at first a fish (i.e. a spermatozoon), but the place for its reception, and the matter for its nutrition, are for a time supplied by the female. 'The father communicates the embryo and first rudiments of life, the structure of the

body being already determined and assigned in the animalcules of the male semen in all creatures, which yet receives some alteration according to the different species of animal or female from whence it is nourished. . . . The mother receives the living rudiments of the foetus from the father, retains and nourishes the same, affording therefore a habitation to the foetus, and nourishment by the liquor of the amnios in which it swims.' Boerhaave, however, like so many others of his period, is not the complete preformationist—in fact he is even disposed at times to favour an attenuated form of epigenesis. But this aspect of his work must be dealt with elsewhere.

V

LAST PHASES OF THE PREFORMATION DOCTRINE

BETWEEN *c.* 1730 and 1760 ovism suffered an almost complete eclipse, and animalculism, though still in some favour, was changing in character. All hope that microscopic observation would reveal the existence of homunculi in the seminal animalcula had been abandoned, but attempts to discover a complex organization in these long-suffering particles were by no means discredited, and resulted finally in the effort to establish them on a new footing as *parasites*. In the meantime epigenesis was slowly but surely gaining ground, and would have advanced much more rapidly in popular favour but for the prejudice against any theory which appeared to require the assistance of a creative force with every generation. Amid all this uncertainty the opinions of Haller, the most respected, if not the most eminent, biologist of the time, could not fail to command a considerable following. After some initial hestitations, he finally decided to employ his vast knowledge and experience in an attempt to re-establish the cause of ovism, and the revival of this doctrine in the second half of the eighteenth century, in spite of the researches of Wolff and others, was due to the experimental observations of Haller and Spallanzani, assisted by the perfervid but erratic advocacy of Bonnet. From this point the old animalculism was doomed, and soon disappeared from the literature of biology.

In 1744 Haller begins to devote his attention to what he calls the theories of epigenesis and *Evolution*.[1] He points out that evolution is almost universally accepted on the strength of the work of Swammerdam, Malpighi, Malebranche, and others. Against it must be ranged the facts of regeneration or replacement of lost parts, as exemplified in Hydra, the tail of the Lizard and the limbs of Crustacea. Further, the development of organs such as the heart of the

[1] This appears to be the first use of the term 'evolution' as the equivalent of preformation. The *Oxford Dictionary* gives Bonnet, 1762, as the first.

chick, which begins as a simple bent tube, and only gradually assumes the complex structure of the adult heart, and the formation of the parts of animals and plants generally, have convinced him that evolution is untenable, and that the organs of the body are generated in succession out of a fluid according to definite laws as taught by Aristotle, Harvey, and others. At this stage, therefore, Haller was undeniably an upholder of epigenesis. In 1751, in his criticism of Buffon, whose hypothesis of living organic molecules he had formerly accepted, Haller attacks Buffon on the ground that his system takes no account of variation, and the same objection might have been urged by Haller against preformation. For example, in the blood-vessels of the hand, he says, there is infinite variation. You may make fifty dissections, and not find any two alike. The most fatiguing work in the world is that of reducing the arteries to a general and uniform enumeration. Variation reigns throughout the whole of Nature, and is much more extensive than it has been customary to suspect. So great is it that Haller is almost tempted to believe that in the formation of animals Nature not only had no model, but that she even worked without a plan.

By 1758, however, all this was changed. Haller had completed his work on the development of the chick,[1] and his own experiences as an embryologist had produced the

[1] According to Haller's *Bibliotheca Anatomica*, ii, p. 212, and his *Opera Minora*, i, p. xix, the two memoirs on the chick were presented to the Göttingen Society in 1757 and 1758. They were first published independently in 1758 in two volumes, the transactions of the Göttingen Society having been suspended between 1754 and 1769. In this first edition of 1758 it is stated that Memoir 1 was communicated to the Göttingen Society on Sept. 30th, 1757, and Memoir 2 on Dec. 9th of the same year. In the Preface to the *Opera Minora*, vol. ii, it is announced that Memoir 1 was submitted to the Society as a Latin lecture on Sept. 3rd, 1757, then translated into French and published in 1758, and that the second Memoir was presented to the Society in 1759 [this must be a misprint], translated into French and published in 1758 with many additions and corrections. In the Index to the *Opera Minora*, vol. ii, we are informed that Memoir 1 was presented to the Society in 1756 and published in French in 1760, and Memoir 2 was presented on Dec. 9th, 1757, and also published in French in 1760. From this mass of contradictions it seems probable that Memoir 1 was read in September and Memoir 2 in December of 1757, both being first *published* in 1758. Blumenbach asserts that the Memoir in which Haller first announced his confirmation of the ovist doctrine was read on May 13th, 1758. Both figures would seem to be erroneous.

unfortunate result of converting him from epigenesis to preformation. He now says it is almost demonstrable that the embryo can be found in the egg, and that the mother contains in the ovary all the essentials of the foetus. His proofs are a confirmation and extension of the position first outlined by Maître-Jan in 1722. The yolk, he asserts, is the continuation of the intestine of the foetus. The inner membrane of the yolk is continuous with the inner membrane of the intestine, and is thus identical with the inner membrane of the gut generally and the skin and epidermis. The external membrane of the yolk is an extension of the external membrane of the intestine, and is hence continuous with the mesentery and peritoneum. The envelope which covers the yolk during the last days of incubation is the skin of the foetus. It is no absurdity to say that from the beginning, and *before fecundation*, the intestine of the foetus is no more than a small hernia of the membrane of the yolk. Now if the yolk is continuous with the skin and intestine of the foetus, it must be contemporaneous with it, and is truly a part of the foetus. But the yolk was present in the abdomen of the hen, and was a part of the hen, independently of any congress with the cock. Hence the foetus, enclosed in the amnion, must have existed at the same time, although invisible on account of its smallness and transparency.[1] Bonnet's comment on this is that the foetus belongs to the hen and exists before conception, and hence preformation is the natural law of organized beings. On the other hand Blumen-

[1] It is not difficult, with the assistance of Fig. 16, to follow Haller's argument. The 'inner membrane of the yolk' is the endoderm, which it is true does become continuous with the skin and epidermis *after* the gut cavity has been completed. The 'external membrane of the yolk' is the splanchnic mesoderm, and the 'envelope which covers the yolk during the last days of incubation' seems to be the allanto-chorion, which however is *not* the skin of the foetus. Haller's procedure is a typical example of the philosophical method of his time, in which observation and inference had only the remotest relations with each other. For example, the statements—'Now if the yolk is continuous with the skin and intestine of the foetus *it must be contemporaneous with it*', and the '*yolk must have arteries and veins* as without them it could not have been brought into existence', are pure assumptions, and beg the very question he has set out to prove. If these assumptions can be shown to be baseless, as they are, the argument collapses. 'Je ne crois rien à priori, absolument rien', says Straus-Durckheim, and it is a motto which may occasionally be borne in mind.

bach's criticism is that even assuming the soundness of Haller's facts, which still await confirmation, it does not follow that the membranes of yolk and foetus coexist from the beginning, and yet the theory rests on this vital and unwarrantable assumption. He points out, further, that a

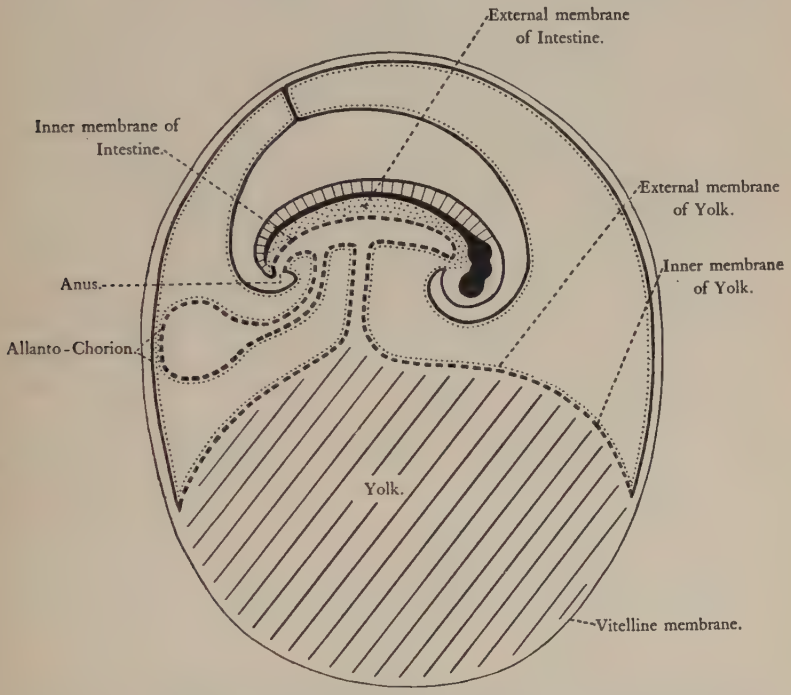

FIG. 16. Diagram constructed to illustrate Haller's interpretation of the foetal membranes of the chick.

plant gall is derived from the surrounding tissues of the plant and is a new formation, and it is therefore probable that the membranes and vessels of the foetus are also new formations —developed from the similar structures of the yolk.

Haller now proceeds to meet possible criticisms. If, he says, it is objected that the yolk has existed independently, and is only later grafted on to the foetus,[1] he can only reply

[1] Paul (1770) meets Haller's argument by asserting that the germ of the cock is

that the yolk must have arteries and veins, as without them it could not have been brought into existence. But these arteries and veins of the yolk can arise only from the mesenteric arteries and veins of the foetus, and the circulation of the blood in them must owe its impetus to the foetal heart. The same blood which circulates in the yolk circulates also in the foetus. It has a common source and a common impulse. The yolk is therefore an essential part of the chick, and since it exists in the non-fecundated as in the fecundated egg, it follows that the system of vessels which unites it with the chick after fecundation must have preceded fecundation also. But if this be so, the chick, which is the end or prolongation of this system of vessels, must also have preceded fecundation. Neither can the membranes of the yolk, which form the intestines of the chick, exist without the chick, of which they form an integral part; and indeed the final stages in the absorption of the yolk take place within the foetus. The yolk therefore is a part of the foetus and cannot exist without it. According to Haller, one of the most powerful arguments in favour of the ovist as opposed to the animalculist theory, is the fact, first demonstrated for the Aphididae by Leeuwenhoek in 1695, and afterwards confirmed in detail by Bonnet in 1745, that an egg which has not been fertilized can nevertheless develop and produce a perfect individual. Here the spermatic animalcule is absolutely excluded, and its importance in generation thereby destroyed. These phenomena struck Haller so forcibly that he reconsidered his views on generation. He did not, however, at first range himself strongly on the side of preformation, even after his observations on the development of the chick, but apparently the influence of Bonnet finally prevailed, and he regarded the doctrine as definitely proved.

To the criticism that in hybrids like the mule the characters of *both* parents are represented, Haller replies that the sperm

grafted on to the yolk of the hen. Such a graft, he says, overcomes the difficulties of generation better than the supposed pre-existence of the foetus in the egg of the hen, and it explains also the continuity of the vessels and membranes of the yolk with those of the chick.

of the male has, as is well known, the power of stimulating the growth of certain parts of the male animal more than others. For example, it stimulates the hair of the beard (but not that of the scalp), the deciduous antlers of deer, and the tusks of the boar and elephant. If therefore the sperm is able to activate some parts more than others in the body in which it is formed, it may be able to do so in the body of the foetus animated by it. It may, for example, drive the blood with greater force in the arteries of the ear or snout, and—the objection is resolved! He admits that this assumption does not explain how and by what mechanism the sperm performs such an office, but he considers he is under no obligation to explain it, provided the facts are established. The specific effect of the sperm on the growth of various organs, he says, is beyond question, although how it discharges this function we may never learn. In summing up Haller says: 'As neither the volition of the individual, nor chance, nor a blind force imparting movement to the organic parts is able to form the organism, we have no choice but to admit that the embryo is already formed before fecundation.'

In the last two volumes of his *Elementa Physiologiae* (1765–6), Haller gives us his final reflections on preformation. He rejects very decidedly the possibility of the existence of seminal homunculi, nor will he allow that the tails of the spermatozoa form the umbilical cord of the foetus. He concludes from repeated observations that the foetus begins to appear much later than is believed—in the sheep not before the nineteenth day. If it occurred earlier he is convinced he would have seen it. The lack of a visible consistency probably explains the difficulty of finding it, rather than its small size. As regards the earliest rudiments of the foetus, he despairs of resolving such a problem. Its investigation is a thankless task, in which the observer is plunged from twilight into intense darkness. It is full of obscurities and beyond our senses, and has given rise to a number of conflicting opinions, none of which is satisfying or solidly established.

Haller now admits, as the result of numerous experiments, that when the chick first appears it is a small shapeless worm, with a huge hernia arising from its intestine, but without signs of beak, limbs, viscera, or even heart. Some hours after, we can distinguish the heart, and then in succession the eyes, liver, gall-bladder, kidneys, stomach, and intestines, and lastly the lungs. We must, he says, not conclude that these parts did not exist before, but that they were so transparent that their outlines could not be recognized. Similarly, at the beginning of incubation, the heart has only one auricle and one ventricle, and by an insensible progress the four-chambered heart is produced. It would thus appear that the young chick arises gradually by various stages, and so passes into the adult animal. Nevertheless epigenesis is totally impossible! The foetus can never have been without a heart, since in the heart resides the principles of all life and movement, and the heart in its turn cannot exist without arteries and veins. These and other parts, however, cannot be seen in virtue of their fluidity and transparency, but are not in themselves too small for observation. When the gall-bladder becomes green with bile and red blood appears in the vessels, these structures at once become visible, without necessarily undergoing any increase in size. Hence there is no region of the animal body made before another, and all are formed at the same time. Even the beard, the horns of deer, the mammary glands and the second teeth exist as latent structures before they become conspicuous during development. He therefore categorically recants anything he may have said previously [in 1744] against the theory of evolution or preformation.

The next problem considered by Haller was emboîtement—whether the ovaries of Eve or the testes of Adam could include the germs of all future generations of the human species. His reply, in brief, is that in some animals such as the Aphis, Volvox, and the Polype, as many as six generations may be represented at the same time, and if an animal may contain many generations, it is not absurd to claim that it may contain them all. It is not reasonable to expect that a

germ in which encasement can be established should be restricted to five or ten generations. Haller mentions birthmarks, monsters, and the phenomena of regeneration as arguments which have been used against preformation. Regeneration, he replies, so far from telling against evolution is in favour of it, and may be compared with parthenogenetic reproduction. It is due to germs which exist in all parts of the body, but which remain dormant so long as the body is undamaged. When, however, an animal is wounded, or mutilated, the germs in that region receive more nourishment and begin to grow, and since in any particular zone they are adapted to the reproduction and repair of that zone only, it follows that the wound will be healed or the lost part replaced. None of them therefore is capable of reproducing the entire animal. Haller makes use of these germs, which represent his latest addition to the preformation doctrine, to supplement his explanation of the intermediate characters of hybrids, and of secondary sexual features such as the deciduous horns of the deer. The germs of all these parts exist before fecundation, but when influenced by the male semen they begin to grow. Thus the young tend to resemble the male in proportion as the male semen is predominant.

Maupertuis (1744)[1] opposes preformation both in the egg and sperm, the foetus being formed by the union of the male and female prolific liquors in the mass (i.e. inclusive of both solid and liquid parts) by elective attraction, as in the formation of crystals. The essential points of the preformation doctrine, as apprehended by Maupertuis, may be summarized as follows: Fecundity, according to the ovist, resides only in the female. The eggs ordained to produce males

[1] Maupertuis is the author attacked by Voltaire in his *Diatribe du Docteur Akakia.* The physician whose name suggested this title was Dr. Martin Akakia, who died in 1551. His name was Sans-Malice, which he translated into the Greek Akakia, the latter version being retained by his descendants. He was sufficiently famous to be known to Voltaire, who took advantage of the meaning of the Greek word when he framed his contemptuous title. It is generally stated that Maupertuis was so humiliated by Voltaire's satire that he died of chagrin. The *Diatribe*, however, was written and published in 1752, and Maupertuis died in 1759, but it was not the only attack which Voltaire directed against the failing President.

bear a male foetus only, but those which are due to become females contain not only that female with its ovaries, but in those ovaries are other females completely formed, and in those again still others, and so in a gradually diminishing series to infinity. These foetuses form a chain of minute statues without life, and to animate them it is necessary to infiltrate them with the vital principle. This is supplied by the seminal liquor of the male, which therefore converts automata into men. The discovery of the spermatozoa completely changed the situation. The foetus, which *imagination* only found in the egg, was actually *demonstrated* in the seminal liquor of the male. It is true that its appearance was rather that of a fish or tadpole, but this was neither new nor surprising, since the eggs of so many animals hatched out as forms quite unlike the parents. The fecundity which had been attributed to the females was now transferred to the males. If a sperm is to develop into a female it lodges only the body of that female, but if into a male it contains a series of males diminishing to infinity. In criticizing this perversion of preformation, Maupertuis fails to observe that both views condemn the luckless organism to extinction, since the ovist makes no provision for the future production of males, or the animalculist for the future production of females. Moreover, the statement that females produce only females is so obviously contrary to fact that it cannot have played a part in any preformation doctrine. Again, where does Maupertuis suppose the male egg or the female sperm to come from ? Maupertuis rejects animalculism because it places an enormous strain on credulity, owing to the infinity of sperms present in the male semen. A writer [Leeuwenhoek] calculated that in the seminal fluid produced by a pike in one act of generation there were more pikes than men on the earth, assuming that the whole world was as thickly populated as Holland. How appalling, therefore, he says, must be the number when one considers subsequent acts of generation, and the supposition that each sperm is itself housing countless others. It can only be described as fecundity absolutely without limit, and

yet in spite of it we know that the number of young pikes produced is strictly limited. So senseless and limitless a slaughter reduces to utter futility this method of generation. Again, does this theory, he asks, make it easier to solve the problem of generation than the theory of new formation [Epigenesis]? It is true we do not understand how in each generation an organized being can be formed anew, but do we understand it any better by assuming that an infinite series of animals contained one within the other has existed from the beginning of time? Both explanations leave the real problem untouched.

We may now trace the growth of the opinions of Charles Bonnet, who occupies in the theory of preformation a position analogous to that of Huxley in respect of Organic Evolution. Just as Huxley expounded and popularized the work of Darwin, so Bonnet embroidered and disseminated the observations of Haller and Spallanzani, and did more even than they to resuscitate the doctrine of ovism in the latter half of the eighteenth century. In his first work of 1745 he observes, in dealing with the generation of organized bodies, that philosophy has invented the beautiful theory of germs, contained one within the other, which develop in succession. He holds that this theory is confirmed by the discovery that certain animals can be multiplied by cutting them into pieces. He says no more on preformation in this treatise, which was published when he was only twenty-five years of age, and is an enduring monument to his genius as an observer, but he is familiar with the work of Malpighi, Swammerdam, and Leeuwenhoek, on which he apparently bases his own conclusions. It was, however, soon after the completion of the *Insectologie* that Bonnet's views on generation began to take shape, and they were published for the first time in Chapters I–VIII of his *Considerations*, which appeared in 1762. These chapters, he says, were the product of his youth. In the original draft he does not use the word preformation, but pre-existence and miniature. It is difficult to define the convictions of a kaleidoscopic and youthful mind, and Bonnet in the *Considerations* passes from doubt

to assurance with such facility and haste that it is not easy to keep pace with him. The following abstracts[1] illustrate this point. The series of infinitely small creations one within the other, he says, which the hypothesis of emboîtement presupposes, overwhelms the imagination without startling the reason. . . . Reason contemplates with pleasure the seed of a plant, or the egg of an animal, as a small world peopled by a multitude of organized beings destined to emerge in a definite order to the end of time. It is not necessary to suppose an emboîtement to infinity, which would be absurd. The divisibility of matter to infinity which has been assumed to be essential to emboîtement is a mathematical truth but a physical error. All bodies are necessarily finite, and all their parts are determinate, but the limits of this determination are absolutely unknown to us, and it is this same ignorance which should prevent us from regarding as impossible the enclosure of germs one within the other. Nothing is more obvious than that matter is prodigiously divided. The scale of organized beings is the scale of that division. How many times is the mite contained in the elephant, the water flea in the whale, and a grain of sand in the globe of the earth? Can we therefore treat as absurd the theory of emboîtement? Volvox is a direct and beautiful proof of encasement. Spallanzani observed three generations at the same time 'in that admirable animal'. Others had been able to see further still, and had discovered a fifth and even a sixth generation, all of them being one inside another, and developing in succession. The budding of Hydra is an example of a number of diminishing generations which represent in the most exact manner a 'genealogical tree'. Is it not manifest that all these generations must have been enclosed in the mother polype? Evolution (preformation) is the principle which best conforms to the facts and to a sound philosophy. The germ 'is an animal, so to speak, in miniature: all the parts which members of its species have full sized it has on a very small scale'. He is persuaded more and more of the pre-existence of the germ in the female, and that the male

[1] These have been assembled from various parts of the work.

semen engenders nothing. In fact there is no generation at all properly so-called, but only a simple unfolding. However, there was at first always lacking the *demonstration* that the germ belonged to the female, that it pre-existed fecundation, and that evolution was the universal law of organized beings. This demonstration for which he had been waiting, and which he had predicted, was announced in 1757 by Haller. He himself had never accepted the view that the time at which the parts of the organized body begin to exist can be judged from the time that they begin to become visible. The stillness, smallness, and transparency of some of these parts may make them invisible. The discovery of Haller demonstrated this great truth, and he hastens to express his appreciation in a letter. 'Your hens', he says, 'enchant me.' He claims in this letter to have formulated the doctrine of pre-existence in a former letter to Haller as early as 1747, but he had not been able to put it to the test of experiment owing to the failure of his eyesight, following the strain of his work on insects in 1745, which had been so serious that he could not even prepare his own manuscript.

In these passages Bonnet is the complete preformationist, but he is by no means always in so confident a vein.

'Whilst the chick is still in the form of a germ', he says, 'all its parts have a form, proportion, and position which differ considerably from those they will ultimately assume. *Consequently if we could enlarge it at this stage it would not be possible to recognize it as a chick.*[1] . . . Thus the germ is extended in a straight line and looks like a spermatic worm, it has only a large head and a slender tail which conceals the rudiments of the trunk and extremities. . . . Observations on the incubation of the egg demonstrate that all the parts of the germ do not develop simultaneously and uniformly.'

When Bonnet wrote these words, therefore, he did not believe that the foetus was a preformed and exact miniature of the adult, since even if all the parts had been present in it they could only acquire their specific shape as the result of metamorphosis or epigenesis. In another place he expresses himself even more strongly: 'All that I have just expounded

[1] Italics inserted.

on generation you may regard if you wish as nothing but a romance. I am myself strongly disposed to look at it in that way. I feel that I have only imperfectly explained the phenomena. But I ask, can you find another hypothesis which will explain them better?' Nevertheless he is 'not prepared to abandon so beautiful a theory as that of pre-existence in favour of purely mechanical explanations'. If development, he urges, should seem to be accomplished by epigenesis, 'our senses deceive us. A mask of falsehood obscures the whole face of nature. Development is a complete illusion, or what appears to arise only emerges from a state of invisibility to one of visibility'. His convictions, however, are again disturbed by reflections on the nature of hybrids. When a he-ass is crossed with a mare the result is a mule. But the foetus already existed *as a miniature horse* in the ovary of the mare. How was it metamorphosed? Whence came its long ears, and why did the tail lose its hairs? He assumes that the male semen has elements or molecules corresponding with the different parts of the foetus, but those molecules which stimulate the growth of the ears are more numerous and active than their analogues in the foetus, and *per contra* the male semen has less elements for stimulating the tail than has the foetus. He admits that it is difficult to understand how such great changes can be produced by the simple action of the seminal fluid. There are also other difficulties. The mule is a large ass rather than a degraded horse, and if a cock be paired with a duck the hybrid has the feet and general characters of the cock. This, he says, would seem to suggest that the foetus after all is not in the female but in the male, but the definite observations of Haller and Spallanzani to the contrary do not permit us to return to that supposition.

Bonnet endeavours to explain on the basis of preformation the phenomena of regeneration, which he had investigated so successfully in 1745. The germs of the higher animals, he says, are confined to definite organs of the body—the ovaries, but in worms and polypes they are scattered throughout the tissues generally, and are hence able to reproduce

the organism at any point, and replace lost parts or organs. He realizes the defects of this theory. Why should an animal reproduce at the head end, a head only, and at the tail end, a tail only, and, more surprising still, why should a tail be regenerated at the head end? To meet these cases he multiplies or reduces his germs, lops off their heads, rushes up the appropriate stimulus to them at the right time and place, and is in fact ready to meet and vanquish any difficulty which may arise with the confidence and dispatch of the modern geneticist. 'But all this', he admits sadly, 'is only conjecture, and I will no longer insist on it.'

In the *Contemplation* of 1764–5, Bonnet returns to a consideration of encasement. The great and the small, he says, are nothing in themselves, and exist only in our imagination. It is possible that all the germs of any one species were originally locked up one in the other, and develop from generation to generation, following a progression which geometry must determine. He then gives the following definition of encasement:[1]

'The term "emboîtement" suggests an idea which is not altogether correct. The germs are not enclosed like boxes or cases one within the other, but a germ forms part of another germ as a seed is a part of the plant on which it develops. This seed encloses a small plant which also has its seeds, in each of which is found a plantule of corresponding smallness. This plantule itself has its seeds and the latter bears plantules incomparably smaller, and so on, and the whole of this ever diminishing series of organized beings formed a part of the first plant, and thus arose its first growths.'

The hypothesis of emboîtement, he adds, is one of the most striking victories of the understanding over the senses. The terrifying calculations by which it has been attacked prove only that it is always possible, by adding zeros to units, to crush the imagination under the weight of numbers. The mechanism of the unfolding is explained by Bonnet thus: It is well known that the eggs of virgin hens grow, and it is now demonstrated that the germ pre-exists in them. Hence this germ grows also, but it encloses others which grow with

[1] This definition is repeated in a letter to Spallanzani dated November 29th, 1780.

it and through it. We may well presume that germs of such inconceivable smallness are not nourished by that lymph which is extracted from the substance of the blood of the great organized whole which encloses them. This lymph, however subtle one may suppose it, would be much too coarse to be admitted into the infinitely slender vessels of the germs. But we may easily conceive that the nervous fluid of the great whole may comprise nourishing molecules of different orders, corresponding with the different members of the series of germs, which molecules the vessels of the germs extract and work up.

Incorrigible speculator as he is, Bonnet is not unmindful of the expediency of basing theoretical views on observation. He says:

'If I have devised some reasonable principles to explain the production of mules such principles will assist in explaining all [inherited] resemblances of the same kind. They rest always on the important observation of the pre-existence of the germ to fecundation [preformation]. I hold, then, that if this observation is ever demonstrated to be false the edifice which I have attempted to build on it will become as ruinous as those I have attempted to destroy. Such is the fate which threatens analytical works. If the fundamental principle is destroyed and the chief link of the chain removed, the whole work becomes no more than a series of propositions more or less erroneous, and it can only be regarded as a pure romance.'

The *Palingénésie* of 1769, apart from certain matters of detail, gives us Bonnet's mature views on generation. The doubts as to the soundness of his opinions which are found in his earlier works have, however, not entirely disappeared, but he claims that his 'ravishing system' has stood the test and is all that he could have expected. Huxley (1878) attempts to show that in the *Palingénésie* Bonnet more or less modified his views on preformation, and admitted that a germ 'need not be an actual miniature of the organism; but that it may be merely an "original preformation" capable of producing the latter'. The passage from Bonnet quoted by Huxley does not admit of the interpretation which he attaches to it, and an examination of the context makes it clear that Huxley

was mistaken, although, it is true, Bonnet did not maintain, and had never maintained, that the germ transmitted an exact model of the adult. Bonnet's latest definition of preformation may be summed up as follows: If everything has been preformed from the commencement, if nothing has been engendered, if what we improperly call generation is only a type of development which renders visible and palpable what was formerly invisible and impalpable and more or less different from that which comes under our senses, it follows either that the germs were originally encased one within the other, and included the elements of all the organic parts in miniature [emboîtement], or that they were originally disseminated over the whole of nature [panspermism]. 'I have not decided between emboîtement and dissemination. I have only allowed it to be understood that I incline towards emboîtement.'

Bonnet essays two new speculations in this work. (1) The germs are imperishable. If they do not develop in the present generation, they contain others which will develop in a future state. When an animal dies and decomposes, its indestructible germs are released, and then pass without the least alteration into the soil or another body, from thence into a second body, a third, and so on. He omits to state what the final objective of their wanderings may be, but tails off into generalities about the province of reason and the philosophic eye. (2) The resurrection of the body may be explained by assuming that it is composed of an essential, imperishable, ubiquitous basis or framework, which is unaffected equally by development or by death. The visible body consists of this reticular basis vastly expanded by nutrition, i.e. by the accumulation of non-essential matter in its interstices. Death results in the destruction of the non-essential body, and the consequent shrinkage or involution of the essential framework to the original infinitesimal proportions which it had in the germ, but it is not dead, and is capable both of immediate reincarnation and ultimate resurrection. This hypothesis became unpopular when it was realized that a mutilated body would of necessity be mutilated in any reactivated

state, whether material or divine, and to surmount the impasse further germs were postulated and added to the vanishing spectre.

In a paper which was obviously inspired by the speculations of Malebranche, Bonnet (1774) develops his views on the *mechanism* of emboîtement. The very subtle juices of the mother, he says, are reconstructed by the germ, and from them are extracted juices more subtle still. The latter are transmitted to the germ of the second generation, which proceeds to elaborate them further, and to extract juices even more subtle, which are passed on to the germ of the third generation, and so on. Thus as the germs diminish in the series, the more delicate become the secretory organs. Their calibre shrinks in a ratio directly proportional to the involution of the germs, and hence they produce alimentary juices more and more subtle, and 'who knows but that this subtlety may not increase in the last generations until it equals that of fire or ether'. Now if the germs are enclosed one within the other they must all grow proportionately, for if that were not so, and those enclosed preserved their original smallness up to the moment of fecundation, how could they be fecundated, since the seminal fluid, as we know it, would have a different physical status to the germs which it activated. *All* the germs of the series therefore grow in proportion to their position in the series, and they are all nourished in a similar ratio. How is this effected? Not by lymph or any analogous liquor, which would not be subtle enough to penetrate into germs of such astounding smallness. It must be done by a 'nervous fluid', which has a tenuity and activity approaching that of the ether of philosophy, and surpassing by far that of any other fluid which circulates in the animal body. This fluid is carried by the nerves of the mother to the ovaries, where it is distributed to the germs of the first order, and worked up and passed on to succeeding orders as already described. Bonnet, it may be added, applies the theory of emboîtement to the reproduction of animalcula in general.

Bonnet's final observations on preformation are in the

form of letters to Spallanzani.[1] In a letter dated April 4th, 1777, he refers to Spallanzani's failure to discover spermatic worms in the semen of the toad. This fact, he says, demonstrates the falsity of the hypothesis of Leeuwenhoek and Hartsoeker, who had conceived the very attractive idea that these animalcula were the future organism in a very small state. In another letter, dated November 29th of the same year, he claims that in frogs, toads, and newts, and also in the fowl, the egg has been proved to contain the embryo before fecundation. This shows that the sperm forms nothing, and only induces to develop what is already there. He urges Spallanzani to write a treatise dealing with the systems of generation, and establishing the system of the pre-existence of extremely small organized bodies in the female before fecundation. Such a work would finally dispose of epigenesis and other hypotheses born of it.

That it is possible to oppose epigenesis without supporting preformation is exemplified by the speculations of Buffon (1749). He asserts very positively that the chick exists in the egg before incubation in a state of suspended animation. The head, backbone, and even the foetal membranes, can all be distinguished. This is no assumption on his part, but is based on observation—he has opened a great number of eggs, and seen with his own eyes the complete chick in the middle of the cicatricula at the moment the egg emerges from the body of the hen. But, as appears later, the 'complete chick' is at this stage only a particle of animated matter in which no definite organization can be distinguished. At one end there appears to be a head, and the remainder, he thinks, will correspond with the backbone. Nothing more can be made out with certainty. The embryo, however, does not exist *before* fecundation, but, as already stated by Malpighi, it is formed mechanically *immediately after* this act by the male and female organic molecules of the two seminal fluids combining to form an organized body or foetus. Hence a recognizable but very small foetus arises suddenly at a very

[1] In these letters Spallanzani is frequently referred to under the complimentary pseudonym of Malpighi.

early stage, but is not in the sperm or in the unfertilized egg. Nothing, he says, is more false than the assertion that the tadpole is already in the egg of the frog before it has been fecundated by the male. He can understand that the Abbés Spallanzani and Fontana should be attracted by the preformation doctrine, because it has the sanction of religion, but he is astonished that the philosophers and medical men, above all the celebrated Haller, should countenance so feeble a discovery. His own theory, on the other hand, is fully confirmed by the resemblance of children to their parents, and by the intermediate characters of hybrids.

When discussing the propagation of plants, the fertilization of which was not then understood, Buffon's language can only be interpreted as implying preformation of a kind. He seems to believe that the seed holds in miniature the tree which will develop from it, but he goes no further, and will not accept an *infinite* progression or emboîtement. Is such a theory, he asks, any solution of the difficulty? Is it not rather cutting the knot instead of untying it—evading the issue instead of resolving it? To believe such a doctrine is to lose sight of truth in the labyrinths of infinity, and to involve the question in tenfold obscurity by removing it beyond the reach of our vision. In his examination of emboîtement Buffon repeats Hartsoeker's calculations, and concludes that on this hypothesis a man would be proportionately greater, when compared with a spermatic animalcule of the sixth generation enclosed by him, than the universe would be when compared with the smallest atom of matter capable of microscopic resolution. But if this calculation were carried to the tenth generation only, the minuteness would be such as to be beyond conception. To admit that these proportions can represent realities was to sanction the absurd. Hence the value of the hypothesis dwindles in proportion as the object fades away. Buffon's own system ignores both the egg and the sperm. In the viviparous animals, he says, the foetus cannot pre-exist in the egg, since there is no evidence that they possess eggs—indeed the non-existence of the egg in the Vivipara amounts almost to a certainty.

Gautier d'Agoty (1750), justly famous as an artist and colour printer, is much less admirable in his operations as a naturalist. He rejects the views of both ovists and vermiculists on grounds which were familiar at the time, his own explanation being that the foetus arises in the seminal vesicle of the male from material supplied by the blood and the testes, and that it reaches the uterus of the female during coition. One or more of such foetuses can be found in the seminal fluid of the male, and they are true foetuses in all their parts. Hence the father provides the embryo completely formed, and it proceeds to grow and become mature in the uterus of the mother. Gautier, however, is not a vermiculist, since his foetus is not formed from a spermatozoon. Two years later, in a paper on the generation of frogs, this speculation is developed and somewhat modified. The embryos are produced by the male frog in a vesicle [urinary bladder] situated in the abdominal cavity, to which vesicle each embryo is attached by a fine thread.[1] The embryos are strewn over the eggs in coition, feed on them for some days, and preserve the same shape that they exhibited in the vesicle of the father for about one month. The tail of the tadpole is formed by the united posterior limbs of the foetus. When the embryos in the frog's vesicle were discovered, he says,

'I was transported with joy—I called to see it all those who were in the neighbourhood. I would willingly have called all the earth to witness a phenomenon so new, so unknown up till now, so extraordinary, and so adapted to convince all those who had doubted the truth of my first observations, not being themselves able to make them. . . . Pythagoras would have sacrificed a hundred oxen to the gods if he had made this discovery. . . . I give my discovery to the public as new.'

He considers that he has destroyed beyond hope of recovery the preformation doctrine. Gautier's ignorance of the anatomy and reproductive habits of the frog is very obvious in this paper, which is severely criticized by Spal-

[1] These 'embryos' were probably the parasitic worm *Polystomum*, which was first described and figured by Roesel in 1758.

lanzani,[1] and his comparison of himself with Pythagoras is appropriately ridiculed by Roesel in his work on frogs.

The foetus in the Vivipara, according to Gautier, is produced in a fluid form in the seminal vesicles of the male, and is compounded of blood purified in the testes, combined with the humours which occur in the vesicles themselves. Such a foetus is discharged by the male into the uterus of the female by a kind of male parturition. In the uterus it is nourished by the semen of the female and the menstrual blood, and condenses into a definite shape. In each seminal discharge of the male there is only one or a few such foetuses. He describes and gives a figure, drawn and coloured from life, of a misshapen foetus observed in a sample of human male semen which had been discharged into a glass of clear and cold water. The only difference between this foetus and one which had been produced in the uterus was the disproportionate size of the head. Similar results are claimed to have been obtained in the ass and the cock. For this discovery he says miscroscopes and lenses are unnecessary—the eye alone is sufficient for one's instruction. Therefore, the father provides the foetus—but not as a homunculus in a spermatozoon. In 1756, the Gautiers, father and son, produce a further essay after the manner of Dalenpatius,[2] the son being responsible for the plates. This work includes a figure of a foetus discovered in the semen of a horse. It was of the size of a bean, and exhibited the features of a horse quite distinctly. Corresponding results are described in the ass, where the foetus had large ears, in the cock, and in man. Whether the Gautiers invented the whole story, or whether they permitted themselves to be deceived by crude resemblances due to accidental configurations in the discharged semen, might be doubted were the figures not so life-like and

[1] In rejecting the pretended discovery of M. Gautier, Spallanzani says, 'I will not pronounce it to be a mere fiction; I will rather suppose that some fallacious appearance has misled him, in consequence of his inexperience in observing frogs and his ignorance concerning their internal structure, which is exceedingly obvious.'

[2] As the elder Gautier was born in 1717, the son must have been very young when this paper was published.

Fig. 17. Figure of a foetus in the human male semen, after J. Gautier d'Agoty

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circumstantial. This certainly suggests the less charitable interpretation of their proceedings.

'Sir' John Hill, the implacable critic of the Royal Society, published a satire in 1750,[1] which was intended to ridicule the belief of Hartsoeker and others that seminal particles or little embryos or animalcula are distributed everywhere, and may be taken into the body with food or in respiration. He describes how he collected from the west wind a number of these floating particles, and on applying his best microscope he 'plainly discerned them to be little men and women, exact in all their limbs and lineaments, and ready to offer themselves little candidates for life'. This polemic was directed also against Buffon's theory of organic molecules at a time when the homunculus, having been evicted from the egg and sperm, was in process of acquiring a new lease of life by being transferred to the doctrine of panspermism.

The dissertation by Burggrave published in 1751 is significant as reflecting a growing interest in epigenesis, which was now gradually, but almost imperceptibly, taking the place of the old preformation doctrine. Burggrave is an animalculist who recognizes that the early embryo does not contain *all* the organs of the infant. Nevertheless in the incubated egg the parts of the animal begin to show in a few hours after incubation, and hence the sperm is not a complete foetus, but contains the germ only of the future embryo. It is in fact a potential organism, and its latent structure is developed after some delay in the uterus, the spinal marrow and brain appearing first, and the other remaining structures following them. He concludes that the sperm is not a little man, but that it exhibits a type of abstract preformation which does not admit of microscopic verification. Lieberkuhn (1751) is another animalculist, who sums up his beliefs in the dictum 'ex animalculo fiat foetus'. The embryo is the product of the seminal animalcule lodged in the egg, and he adds a new feature to this familiar picture by announcing that the tail of the animalcule forms the backbone of the

[1] This little work enjoyed a considerable vogue, and has even been reprinted in modern times.

future foetus. Parsons (1752), on the other hand, is an ovist but not a preformationist. The male semen, he says, acts as Harvey believes—not by direct contact but by intangible penetration as an 'effluvium'. 'Therefore it would be extreme nonsense to imagine that the insignificant animals, commonly called spermatic animals, can contribute anything towards propagation. . . . But such low conjectures deserve not to be confuted by argument.' His objection is that it is physically impossible for the male semen to reach the egg as a *material* substance, but how it reaches and affects the ovum as an effluvium is equally inscrutable, and this process he concludes 'must ever remain mysterious and unknown'.

The eminent microscopist Ledermüller (1758) rejects Buffonism in favour of preformation and emboîtement in the seminal animalcula. His argument may be paraphrased as follows:

'I venture to say a word on the difficulties of those who are unable to comprehend that in anything so invisibly small as the seminal animalcules all the internal and external parts of a man can be hidden. To establish this I hope it will be sufficient if those opponents of the importance of the seminal seed will examine a pine or fir or other forest tree. It is indisputable that from the small motile seed the lofty magnificent fir and pine grow, with all their complex structure. If now it must be admitted that all this arises from the seed, and that in the last resort it must all be concealed in the seed, why then is it doubted that in the male seminal animalcule also all those parts are already created which belong to a complete man? Shall the Almighty and inscrutable God be greater in the creation of a plant than in that of an animal, and especially of man? I hold that the small seminal animalcule develops in the mother just as the seed does in the field. In the beginning of the world all sperm, all the first foundations of plants and animals which were to come after, all sperm whether on account of its extreme smallness it can be perceived or not, came into existence.'

The critical sentence in this defence is the claim that the whole tree *must be concealed in the seed*, and it is remarkable that Ledermüller, and for that matter all other preformationists, did not realize that if the point to be established is assumed at the outset, all further disputation is superfluous.

The position taken up by Wolff (1759) will be considered in the chapter devoted to epigenesis, but in the meantime a contention of fundamental importance on which he insisted must be referred to. He attacks the statement made by the defenders of emboîtement that the encapsuled foetuses cannot be seen because they are too small and transparent. To this Wolff replies that microscopic observation justifies the assertion that the earliest phases of animal development *can* be seen, and when seen they are entirely inconsistent with any theory of preformation. It is obvious that Wolff is reopening the controversy on grounds which admit of a definite decision being reached. The statement, however, that the *earliest* phases of development can be seen is itself an assumption, which may or may not admit of proof, and on that basis the argument must proceed; but if the first *observable* phases are not reconcilable with a preformed organism, a verdict in favour of Wolff's conclusion, that the preformation doctrine is a fable, must be recorded.

Astruc (1765) enjoys the doubtful honour of being the last of the animalculists, and as such commands the sympathy of the historian, but he is not the complete animalculist. It is indisputable, he says, that both sexes contribute nearly equally to the embryo. Fertilization takes place in the ovary, where the most nimble of the seminal vermiculi passes through a chink in the tunic of the ovary, and then through another chink into the egg beneath it. The chinks associated with the ripe eggs are larger and more widely open, and hence such eggs are fecundated before others which are less ready. The subsequent growth of the egg is stimulated by the oscillatory movements of the vermiculus. Finally, the egg escapes from the ovary, descends to the uterus and becomes the embryo. The foetus is produced by the vermiculus, and hence belongs to the father, whilst the egg is responsible for the placenta, which is therefore maternal. This conclusion inspires the following reflection: 'It is said with truth that death levels all distinctions, but one may say with greater truth that our origin indeed humiliates us, for we are all of us only vile insects which among a thousand

million other similar insects have been more active or more fortunate, and, having penetrated the puny vesicles of the ovary, have developed and been found worthy to receive the Divine endowment of a spiritual soul which elevates us to the dignity of man.' He is impressed by the millions of vermiculi pitilessly condemned to destruction for every one which is sufficiently happy to enter an egg, but he admits that it is a law of Nature to multiply germs in order to ensure the preservation of the race. To those who regard the vermiculi as little men this wholesale slaughter is alarming, but he affirms that they are not homunculi, but vile insects similar to myriads of others abounding everywhere, and hence their destruction is of no consequence. Nevertheless, in another part of the same work, Astruc allows a certain complexity in the seminal animalculum, and before it unites with the ovum it has a real circulation, which is the same as that of the foetus, or even of the adult itself. The animalcule is a human creature, but with the exception that it does not respire, and therefore its circulation avoids the lungs as in the foetus. In still another place he states that so far from the vermiculus being a well-formed little man, the embryo itself some days after conception, though bigger than the vermiculus, is yet only a little mucus attached to a thread, which is without form, and in which no definite outlines can be distinguished. The contradictory nature of these and other passages would indicate that when Astruc wrote this work his opinions were still at the fluid stage.

In defending the animalculist position, Astruc contends that the vermiculus is responsible for such paternal characters as are transmitted to the progeny, the maternal qualities being reproduced by moulding during fertilization, as described in the lecture notes of 1743.[1] To the objection that this scheme of inheritance may explain physical resemblances between parents and offspring, but not those of temperament and constitution, he has no reply, but adds that this may be one of the mysteries of generation which even long continued study will not solve. Sex is explained on the assump-

[1] See p. 83.

tion that the vermiculi are either male or female, the male being the larger. The chink in a particular ovum may be too small to admit a male vermiculus, and therefore a female embryo is selected. If on the other hand the chink is large enough to admit the male vermiculus it would also admit the female, but it would be too big, and hence the female vermiculus would be tossed about and perish, being unable to fix itself in the egg.

It should be noted that Astruc is writing after Wolff, whose dissertation was published in 1759. He does not mention Wolff by name, but he is antagonistic to any formation of the embryo by the 'reunion of different parts of the semen', or by 'the fortuitous concourse of blind atoms'. He then asks—are all the parts of the body formed successively by God every day as they are required, or were they all formed by Him at the time of the Creation, in which case by what means have they been handed down? To these questions he admits there is no answer, but points out that very few naturalists have adopted the first opinion [epigenesis]. 'The *common opinion* is that God has created all men who have been, who are, or who shall be, in creating Adam; that they were all enclosed one within the other in the vermiculi of Adam; that they have been all unfolded one after another in their proper turn; and that they will be unfolded continually, in the same manner, so long as the human kind shall exist.' His comment on this is that those who maintain such an opinion must be alarmed at the almost infinite smallness existing men, and still more those of ages to come, must have exhibited in the body of Adam. Imagination cannot keep pace with such a calculation, and the theory, he says, is only a vain chimera.

Voltaire's criticism of animalculism (1767) is that of the amateur and man of letters. Can we believe, he says, that the little men (homunculi), which are so active in the semen, are doomed to inactivity after entering the egg, and in man must remain so for nine months? This seems to him inconsistent and to be at variance with the nature of things, and he dwells on this curious objection at some length. Later, in

1777, he returns to the point. How, he asks, could the little men which run about so nimbly in a drop of semen be expected to remain motionless for nine months in the mother's womb? Their very activity makes it impossible for them to accept such a role. Apart from this it is repulsive that man should first be a caterpillar, and like it pass through a metamorphosis before reaching the adult state. After considering the rival hypotheses of animalculism and ovism Voltaire concludes: 'On sera peut-être enfin obligé d'en revenir aux oeufs, après avoir perdu bien du temps,' and to the question—what has been the result of all these disputes? he replies briefly 'le doute'. In 1768 he mentions that the system of eggs was accepted for some time, and was supported by the daily and incontestable testimony of some species (chick and frog), but that now the system of spermatic animalcules was supplanting it.[1] 'Cependant,' he adds, with unimpaired cheerfulness, 'on a fini par douter de l'un et de l'autre.' He is certain, however, that reproduction is by germs, whichever system may ultimately prevail.

The great reputation as an experimenter and a philosophic naturalist which was deservedly enjoyed by Spallanzani adds considerable importance to his pronouncements on generation. According to Pouchet, the most weighty opponents of spontaneous generation ranged themselves under the standard of Spallanzani, who to them was almost a prophet. At first (1765),[2] he has no very definite opinions of his own, but is more sympathetic towards the ovists. He accuses Leeuwenhoek (quite wrongly) of asserting that the spermatozoa have all the characters of animals—a head, a bust, and a tail, but he regards such statements as efforts of the imagination. In his *Prodromo* of 1768, he claims to have discovered the existence of the tadpole in the egg of the frog *before fecundation*, and he is now definitely an ovist. The frog is hence not oviparous but viviparous. This 'discovery' is not de-

[1] Voltaire's knowledge of the literature is at fault here.

[2] It is interesting to note that Spallanzani, like Leeuwenhoek, preferred the simple microscope, which, he says, resolves with ease and accuracy the finest and most subtle details of the objects examined. He employs the compound microscope only for low power work.

veloped in the *Prodromo*, and it was not until some years later that he made use of it to support preformation views in embryology. In 1776 he discusses Leeuwenhoek's opinion that the spermatozoa are the immediate authors of generation, according to which opinion the spermatozoa of man are so many homunculi, those of the bull so many vituli, and those of the horse so many foals. He admits that the idea is very ingenious, but adds, 'it is unfortunate that it is not true'. He claims to have confirmed Haller's 'beautiful discovery' that the foetus belongs to the female, and *that it pre-exists fecundation*. Hence the spermatozoa cannot be foetuses. He remarks that Haller's facts are so convincing that it is impossible to withhold assent to his conclusions. Spallanzani brings some new observations to bear on the theory of emboîtement, which he confirms by his investigations on *Volvox*. In this animal he saw three generations of enclosed individuals, and he mentions that some observers had found five, but that he himself could discern no more than three at any one time. He traced the successive emergence of thirteen such generations, and this he claims overcomes the difficulty of comprehending the envelopment of animals in animals—a doctrine which may startle the imagination, but does not confound the reason.

In 1780 Spallanzani follows Swammerdam in holding that the embryo develops from the *substance* of the fertilized egg. 'The tadpole of the frog', he says, 'does not come out of the egg but the egg is transformed into a tadpole; or, to speak more philosophically, the egg is nothing but the tadpole folded up and concentrated. As the result of fecundation it is evolved, and displays the features of the species.' The black and white egg of the frog is *not* an egg but a tadpole or foetus. His train of thought seems to be that as the tadpole cannot be visualized as the product of epigenesis, there is no alternative to the conclusion that it was there all the time. This false step involves a further error, for, he says, since the structure of the uterine egg differs in no respect from the just fertilized egg, it follows that the foetus was present in the egg before fertilization. 'The identity between the

impregnated and the unimpregnated ova is manifest. But the former are nothing but foetuses of the frog, and therefore the latter must be so too. Hence the foetus exists in this species before the male performs the office of fecundation.' Spallanzani therefore subscribes completely to the doctrines of preformation and emboîtement in the egg. It is strange that a man who was such a shrewd observer and thinker should have so confused the processes of observation and reflection. The fact, however, that he was one of the first to describe the cleavage of the fertilized ovum can hardly be expected to have had much significance in the case of a worker living at that time. Having taken one false step Spallanzani proceeds to involve himself in further difficulties. The eggs in the ovaries are regarded as foetuses, and are present in that form in the ovary at least a year before they develop and are shed. The foetuses which appear in the ovary year after year are not successively generated, but existed all the time, and they are only unfolded and become visible as they are wanted. He concludes this on purely speculative grounds. 'Is it not infinitely more philosophical to suppose that the limbs co-exist with the tadpoles, and are invisible only because they are too small to notify the senses? And if it is reasonable to adopt this opinion concerning the limbs, shall we not also admit it with respect to the foetuses of the tadpoles?' When Spallanzani is accused of asserting that both unimpregnated and impregnated eggs contain tadpoles he becomes very subtle. 'I do not say', he explains, 'that I have found the tadpole to exist as well in the former as in the latter egg, but that both are nothing but tadpoles.' He maintains this view in defiance of the facts of development in the frog and chick, which up to a certain point he had correctly observed on his own account, and claims further that preformation is to be found in plants as well as in animals. Spallanzani diluted semen to about one three-thousandth of its bulk, but found nevertheless that a single drop of the diluted semen was capable of effecting fertilization. He argued from this that as the amount of semen in the drop was infinitesimal, it could have added

nothing *material* to the egg, and hence the semen acts as a stimulus to the foetus preformed in the egg, and only sets in motion that series of growths which finally emerges as the visible foetus. He went even further, and maintained that the male semen did *not* lose its fecundating properties even when deprived of the seminal animalcula, but his experimental methods were not sufficiently developed to demonstrate this point. Spallanzani's last contribution to the theory of generation was published in 1784. His views had not changed, and he now concludes, on grounds similar to those adopted by Haller in the case of the chick, i.e. continuity of the membranes of foetus and egg, that the foetus may be demonstrated to exist in the egg previous to fecundation in the torpedo. Thus, he says, a new argument in favour of pre-existence in the ovum is brought to light. Haller had previously shown it in the chick, he himself in various Amphibia, and now the torpedo is added to the list. He has no doubt but that it represents a general and a luminous truth.

An unexpected interlude is supplied by the work of Pirri (1776). In criticizing the preformation views of Haller on the chick and Spallanzani on the frog, he asserts that the tadpole and the frog are stages of two different animals. Spallanzani in reply dismisses this statement as a 'harmless mistake', and Haller sagaciously observes that 'it is always dangerous to attack observations by argument'. Bonnet in a letter to Spallanzani says that 'an opinion so singular does not deserve to be anxiously confuted, and every naturalist will excuse you from taking much pains for that purpose'. Priestley (1777), more perhaps on theological grounds than anything else, follows the 'excellent philosopher Bonnet', and swallows emboîtement without misgivings. On the other hand Gleichen (1778) argues strongly against preformation in egg or sperm, and stigmatizes it as a pure conjecture, based on a tissue of errors, deductions, and explanations the most bizarre. It has only succeeded, he says, in relegating the most important aspect of Natural History to its ancient chaos of uncertainty. Patrin also, the supposed author,

according to Blumenbach, of a 'most ingenious and witty' treatise on generation (1778), attacks preformation, but does not examine the doctrine in detail. The first important criticism of preformation, however, comes from Blumenbach (1780), to whom Kant ascribes the chief credit for establishing epigenesis. According to the ovists, says Blumenbach, we are all much older than we supposed ourselves to be, and we are all of the same age, that is about six thousand years. He admits that he was at first so impressed by the observations of Haller and Spallanzani that he adopted ovism, but he became convinced of the fallacy of this doctrine by his experiments on a 'green armed polypus', which had a 'long spiral body' and 'short and rather immovable tentaculae' [*Hydra*]. When this animal is divided up, each portion grows into a complete individual with arms, body, and tail. He concludes from this and other experiments of a similar nature that 'there is no such thing in Nature as pre-existing organized germs'.[1] The seminal matter is unorganized, but at the appropriate moment it is taken over and subsequently controlled by a vital principle which he calls the *Nisus formativus*. Blumenbach's criticism of Spallanzani on the frog is that it is a waste of time to refute an assertion the falsity of which can be established by any intelligent person every spring. He pours ridicule on certain abnormal occurrences which were quoted in support of preformation, such as that described by a well-known physician, Dr. G. Clauder, in 1685, the phenomenon itself having occurred in 1672—the year Swammerdam first published his views on preformation. In this case a woman gave birth to a large female child. Parturition was completed without incident, and the child had all its parts normally developed, except that its abdomen was distended to an extraordinary extent. At the end of eight hours it was taken with violent abdominal pains, as shown by its tears and agitation, and after the ejection of some blood and water it was delivered of a female child, the birth being accompanied by all the normal phenomena, including the

[1] Blumenbach describes grafting the anterior half of a green Hydra on to the posterior half of a brown one.

subsequent discharge of a placenta. This second child was of the length of a finger, and was so lively that they did not scruple to baptize it. 'These examples', remarks a contemporary reviewer, 'are very rare.' It was considered to prove that even in the newly-born infant the next generation is represented by small but perfect foetuses. Again, the occurrence of dermoid cysts, with their contained bones, teeth, and hair, was well known in the seventeenth century, and interpreted as important evidence for preformation. Blumenbach opposed these cases by others, equally well authenticated, but yet of so flagrantly impossible a character, that he succeeded in reducing this type of argument to an absurdity. He maintains, on the other hand, that the most careful examination never reveals a foetus in the egg immediately after impregnation, nor can the foetus be seen until some considerable time has elapsed. In the case of the chick there is not 'even the most distant resemblance to a chick in the first twelve hours, nor indeed until the end of the second day . . . which circumstance, considering the perfection and powers of our microscopes, is by no means favourable to the theory of evolution [preformation]'. Blumenbach attaches great importance to hybrid animals and plants as proving that *both* parents are concerned in generation, and therefore that the foetus could not have been in either of them. The 'evolutionists' having replied that the sperm, in addition to its stimulative role, may have certain formative powers, Blumenbach replies testily: 'What in the name of Heaven is such a subterfuge but the silent acknowledgement of the insufficiency of the germ theory, and of the necessity of having recourse to formative powers in order to extricate it from its difficulties?'[1] Regeneration was explained by the preformationists as being due to nascent germs scattered throughout all parts of the body, which germs were roused into activity by local injuries. Of all improbable theories, says Blumenbach, this is the most romantic and improbable.

One of the most completely developed statements of emboîtement from the ovist point of view was published by

[1] He forgets for the moment his own 'subterfuge' of the *Nisus formativus*.

Senebier in 1785. Animalculism was then dead, ovism a dying taper, and Buffon's organic molecules had failed to obtain supporters. None the less ovism never had a more convinced and enthusiastic upholder than Senebier, but a cause which has more use for rhetoric than observation, or which mistakes rhetoric for reason, can never keep its place among the principles of Science. Senebier refers to the pre-existence of germs as an important truth, which reason compels us to accept as demonstrated by Haller's observations on the yolk of the egg. 'We lack', he says, 'perhaps only the eyes or the microscopes to see future forests in the acorn or in the seed of the elm.' Such an instructed vision is to that of the Abbé Spallanzani what his own is to that of an ordinary man untrained in observation. The impossibility of perceiving animalcula infinitely smaller than those discovered by the microscope should not prevent us from believing in their existence, since most animalcula are transparent, and it would only be necessary to increase the transparency of those which we can see to make them also invisible. It is easy to imagine animalcula much smaller than any which the microscope has revealed, and there is nothing unreasonable in this supposition.

Commenting on the difficulties of the problem of generation Senebier exclaims:

'In vain a host of ingenious and profound men have assembled observations on this important matter; in vain the boldest genius has analysed this capital question. The passing of centuries results only in a succession of errors, and whilst darkness the most profound has always obscured from the faculties of physiologists the secrets of generation, ideas the most incredible, contradictions the most flagrant, and travesties of nature the most incoherent have constituted the knowledge of those who flattered themselves on explaining the phenomena. Bonnet in a profound analysis has penetrated the course of Nature in this operation. Haller discovered it in his beautiful work on the chick in the egg, and Spallanzani has exposed it in the astonishing memoirs which he has published on this subject. The century of Bonnet, Haller, and Spallanzani produced a precious attempt on the history of generation, in place of those romances which the best minds could read only with disgust.'

Nevertheless, as Blumenbach would have remarked, the

'precious attempt' of Bonnet, Haller and Spallanzani is but one romance more.

According to Senebier, there is only one system of generation worth examining, and that is the pre-existence of the foetus in the female before fecundation—a theory he regards as a law of Nature, and as a naïve and faithful translation of some sublime pages of the Book of Nature. He considers that the researches of Bonnet, Haller, and Spallanzani have established this hypothesis with almost all the rigour which one associates with the demonstration of a physical truth. If, he says, one regards the chick in the egg as in a cradle, where it remains until it is fecundated, can one believe that it lacks the parts which make its existence possible? If this were so it would not be a chick, and no force of Nature could make it one. And if one concedes a single organ to the chick, one must concede all the others as a logical consequence. The observations of Haller have revealed clearly the stomach and intestines of the chick as an extension of the membranes of the yolk, but one cannot admit their existence without accepting that of the liver, lacteal vessels, veins, arteries, heart, muscles, and nerves, which it is true may not have a solid form as we know them in the developed chick, but have a solidity proportionate to that of the corresponding parts in the perfect state. Spallanzani has proved by the most rigorous analysis that the non-fecundated foetuses which exist in the ovaries of the frog are exactly similar to those which have been fecundated—they have all the essential parts of the perfect tadpole, and in consequence they comprehend all the parts of the frog, toad, or salamander, just as the caterpillar in the egg encloses all the parts of the butterfly. Since therefore the foetus pre-exists, and is not the consequence of fecundation, it is evident that it must have been already created with all its organs, and that it has existed in such form before our senses could discern it. When and how was it created? These questions which appear at first to overwhelm us in the labyrinths of metaphysics, may, however, be resolved by simple reasoning. After this confident pronouncement it is disappointing to learn that the

only solution Senebier has to offer is to invoke the intervention of a Creator, and to assume the need of a Creation. Nothing is created anew, he says, and all the foetuses were created at one and the same time, and have since that time emerged in succession to populate the earth with animals and plants. Let us therefore admire the Author of it all, who at the moment of the Creation of organized beings created in one 'vaste enceinte' all generations to come, as long as the planet on which we live shall endure. If, he adds, the term emboîtement, which has been employed to represent the succession of foetuses of organized beings enclosed in females, does not express clearly what one would wish to convey by this word, the event must not be judged by the symbol. Certainly the word emboîtement has never signified an encasement similar to that represented by a series of boxes placed one within another.[1] What one understands by it, for example, is that a seed of the elm contains the elm to which it will one day give birth with all its branches and seeds. Each of the contained seeds will thus include another elm with its branches and seeds, and so on for all generations to come. Hence the *daughter* of Eve, from whom the reader of Senebier is assured that he is descended, enclosed a series of foetuses less considerable than that of her mother who contained them all, for with each successive generation they decrease in number.

Kant (1790) is opposed to preformation and to any mechanical conception of the origin of life. The theory of preformation, he says, 'removes every individual from the formative power of Nature in order to make it come immediately from the hand of the Creator . . . as if it were not all the same whether a supernatural origin is assigned to these forms in the beginning or in the course of the world'. Kant holds that epigenesis has great superiority over preformation as regards the empirical grounds of its proof, and in so far as it regards Nature as self-producing and not merely as self-unfolding. Even apart from proof, reason regards epigenesis with particular favour.

[1] In his definition of emboîtement Senebier is obviously following Bonnet.

The opinions of Erasmus Darwin (1794) on generation display more originality than the bulk of the literature on this much debated topic, and his criticisms are often shrewd and to the point. 'The process of generation', he says, 'is still involved in impenetrable obscurity.' In the fowl the unfertilized egg consists only of the yolk and white, which are the food or sustenance of the future chick. The cicatricula is supplied by the cock and is the rudiment of the new animal, but is not a foetus. Hence the embryo is provided by the male, and the oxygen, food, and nidus by the female. He refers to the old and repeated objection of the great wastage of seminal animalcula, but it does not convince him. He points out that young fish perish in countless millions, and they are much more perfect animals than the seminal organisms. There is a general law governing these matters, and it is by a wise superfluity that species are continued. The idea that the semen of the male provides a stimulus to the egg of the female, exciting it into life, has no support from experiment or analogy. The theory of emboîtement, whether in the egg or sperm, is also unsupported by any analogy with which we are acquainted, and ascribes a greater tenuity to organized matter than we can readily admit. The miniature foetuses being supposed to 'consist of the various and complicate parts of animal bodies, they must possess a much greater degree of minuteness than that which was ascribed to the devils that tempted St. Anthony; of whom twenty thousand were said to have been able to dance a Sarabande on the point of the finest needle without incommoding each other'. He also ranges the facts of regeneration against the theory of preformation. A crab can reproduce an entire limb, snails and worms their heads and tails, and hence 'in these animals at least a part can be formed anew, which cannot be supposed to have existed previously in miniature'. Again, the resemblance of hybrids to *both* parents cannot be explained on the emboîtement theory. The primordium or rudiment of the embryo, according to Erasmus Darwin, is secreted from the blood of the male parent, and consists at first of a living filament like

a muscular fibre. His own explanation of the generative process is a modified form of epigenesis.

As late as 1803, and in spite of the fact that epigenesis had made important progress, we find the distinguished Scottish naturalist Dalyell still expressing unabated confidence in ovism, and in the existence of the foetus before fecundation. This, he says, is 'universally known' and rests on 'indisputable observations', and adds that the difficulty of understanding the gradual unfolding of the embryo [epigenesis] was so great that when naturalists were provided with a living animal in the form of the spermatic vermiculi of the male they eagerly adopted it as the principle of existence. Good (1805), however, has little belief in the spermatozoa, which he dismisses contemptuously as 'worms and porwigles' [tadpoles]. He says that the animalculist theory was universally accepted until a very few years back. 'Every naturalist, and indeed every man who pretended to the smallest portion of medical science, was convinced that his children were no more related, in point of actual generation, to his own wife, than they were to his neighbours,' and, in spite of much convincing evidence to the contrary, 'the system of generation *ab animalculo maris* was still triumphantly maintained, and the feeble expressions of the few, who had sense enough to oppose it, were drowned in the multitudinous vociferation of their opponents.'

Oken's work on generation was written when he was a student, but not published until 1805. It is a more sober production than many of his later writings, although his views on preformation remained unchanged. The male semen and the ova, he says, represent the total organism reduced to an elemental menstruum. All life as first created was microscopic and infusorial, and all the larger forms of life have since been formed from the infusorial by development. Decomposition is a dissolution of the body into its constituent elements or infusoria, i.e. reduction from the higher to the primordial life or original chaos. All higher animals are built up from certain ultimate living vesicles or cells or infusoria, which the process of generation assembles to form a new body. Thus the fundamental organic sub-

stance *consists* of infusoria, and *originates*, or is synthesized, from infusoria. There is no preformation, but only a collection of infusorial vesicles which by various combinations produce the different forms of the higher organisms. Generation is consequently synthetic and epigenetic. Every generation begins *de novo*, and not from an organized stage such as a preformed miniature. *Omne vivum e vivo. Nullum vivum ex ovo.* Oken is therefore opposed to preformation either in the egg or sperm. The ovum is an entire animal in idea and design only, *but not in structure.* It is related to the animal produced from it as thought is to the word. The *materials* for the animal are there, and *even arranged into principal masses*, but there is no preformation. In the ovum the animal resides as an impalpable spectre, and not as a minute but corporeal miniature. It follows from this that the origin of the elemental infusoria is not from eggs, but from the dissolution of the larger animals into their constituent parts. It will be noted that Oken is an early, if not the first, author after Harvey to express belief in the intracellular or modern version of preformation.

Cuvier was above all an anatomist, palaeontologist, and systematist, and displayed little interest in such general problems as that of generation. In both editions of the *Leçons* (1805, 1846) he acknowledges that generation is the greatest mystery the economy of the animal body has to offer, and its essential nature is still enveloped in complete darkness. He rejects Buffon's organic molecules, and believes that directly the living body can be perceived, however small it may be, it has all its parts. It is not by the addition of new layers that it grows, but by the development, now uniform and now unequal, of parts entirely pre-existing, by enlargement alone. Cuvier is therefore a preformationist. He recapitulates the ovist and animalculist versions, and concludes that the question is wholly insoluble in the present state of knowledge, and argues that although it has been discussed by physiologists for a long time it would be better to abandon the discussion for a period. In another place he says: 'I speak neither for nor against epigenesis.'

In a later posthumous work (*c.* 1840) Cuvier remarks that in the ovist system all the phenomena of life are produced by a first clash or awakening—the result of the inspiration of the male semen. The association of the foetus with the egg is more manifest and intimate than it is with the sperm. Hence in 'most animals' it has been 'demonstrated' that the egg pre-exists in the mother, and the germ pre-exists in the egg. Cuvier therefore is an ovist, but he is not the last of them. He admits, however, that epigenesis is the more popular hypothesis in Mammals, where the difficulty of observing the first appearance of the foetus has favoured this particular system by failing to establish any degree of organization in the early stages. He also recognizes that the existence of hybrids and monsters can be explained on the theory of epigenesis, but not on that of preformation. Emboîtement strikes Cuvier as appalling to the imagination, but not unintelligible. Philosophers, he says, are bold in speculation, and the divisibility of matter is sufficient to sustain them.

Fray (1817) was not a working naturalist, but a philosopher who had carried out a few personal observations. He hesitates to discuss a doctrine so childish as the pre-existence of germs, which was not worthy of the century in which it prevailed, but nevertheless some very celebrated men had adopted it. Emboîtement, he says, is a very convenient hypothesis, since it dispenses with all laborious research, and reduces the solution of the problem of generation to a single word. It indeed rolls back the difficulty, but it banishes it so far that it seems almost to disappear. Fray's objections to preformation are chiefly that it assumes a state of things which not only cannot be checked by observation, but is repugnant to reason and probability. He describes it as a stream of words and incoherent ideas. 'Where is the intellect which can unravel this chaos?' He attacks the work of Spallanzani on preformation in the Amphibian egg, and challenges his statement that the foetus is there before fecundation. His own view is that the egg is a kind of external uterus,[1] and acts only as a nidus for the development of the

[1] This idea had previously been developed by Buffon.

foetus, and does not itself form the foetus any more than the uterus does. He claims that the tadpole possesses external gills for breathing like a fish, but has no lungs or limbs. How therefore can the latter organs have pre-existed in the egg? On the contrary they arise by epigenesis only when they become necessary to the animal, i.e. at metamorphosis. Again, have all the stomachs of certain crabs and the skins of reptiles which are shed and lost from time to time pre-existed in the germs of these animals? 'What a confusion of ideas!'

In their first excellent paper on generation Prévost and Dumas (1821–4) remark that the theory of emboîtement with its infinite series at first startles us, but gradually we get used to it, and may prefer it to all the others. It seems easier to conceive a period when Nature by a single effort gave birth to all Creation present and future, than to presume a ceaseless activity. This primitive impulse requires only that each generation should unfold itself according to the physical and mechanical laws which regulate the dead world. Nevertheless they hold that the fundamental idea of preformation is without proof, and must be regarded as a gratuitous hypothesis which concerns only the historian.

Amid all this repetition, speculation, and vain philosophy, any fragment of observation which serves to *test* the preformation doctrine, and transfer the controversy from the platform to the laboratory, is doubly welcome. Such a fragment was supplied by E. Geoffrey Saint-Hilaire in 1822–6, and encouraged the hope that the experimentalist was at last to put an end to the science of words.[1] Geoffrey investigated the bearing of monstrosities on the theory of the pre-existence of germs. The question of the significance of monsters had been debated in the early days of the Paris Academy of Science, and the point was raised, but in the

[1] The following amusing passage from Burdach is not without its modern applications: 'At the beginning of the nineteenth century the system which in Germany they dignified by the name of Nature Philosophy had set their minds in a flutter, and produced a great movement in Science; but it lost itself in the clouds of an imaginary world, and encouraged arrogance to such an extent that good sense was disdained as a quality entirely plebeian.'

absence of experimental data could not be resolved, whether the monster was represented in the germ ('original monstrosity'), or whether it was produced later by conditions obtaining during development. Geoffrey started his experiments in 1820 and 1822, but it was not until 1826, when a large chick hatchery was established at Auteuil, that he was able to conduct experiments on a large scale. The eggs for about the first three days were incubated under normal conditions, but were then brought under abnormal stimulation, such as shaking, perforation, a vertical position either on the broad end or the narrow, or coated with a layer of wax or varnish so as to make the shell impermeable to air. Numerically, the results were not striking, but several embryos were found to present deviations from the normal, ranging from slight to very complex monstrosities, similar in general character to those occurring spontaneously in animals and even man himself. Geoffrey therefore concludes that embryos which under natural conditions would have developed normally, and which even begin to develop normally, may nevertheless hatch out as anomalous and even monstrous individuals. Hence the abnormal features arise subsequently to fecundation, and are not the result of the growth of a pre-existing germ. Their origin is accidental and not primitive—a germ is not predestined to monstrosity. This production of monsters by experimental means Geoffrey regards as decisive evidence against preformation. 'Pre-existence of germs', he says, 'originated as a metaphysical explanation of ill-observed phenomena, and is based on a number of gratuitous suppositions.' No attempt was made to meet Geoffrey's argument at the time, but his results were not accepted at a later date by Blainville, who has been described as the last of the ovarists. Geoffrey's son Isidore, however, repeated his father's experiments in 1836, and although his results were in great part negative, he considered that he had obtained substantial confirmation of his father's statements, and that the preformation doctrine should be relegated to the past history of the science.

When von Baer wrote his celebrated work on embryology

(1828), ovism, the last hope of the old preformationists, was practically dead, but he made its resurrection impossible. The wealth of careful and sound observation which that great work contains reduced to negligible proportions the rhetorical and argumentative methods of the preformationists, and demonstrated, as such work always must demonstrate, that only by observation and experiment can the biologist hope to advance. Von Baer asks himself the question whether the entire embryo with all its parts may not exist on so small a scale as to be beyond the reach of microscope and measurement? He decides against the supposition. He believes himself able to establish that the younger the embryo, the less complex is its constitution. If the tissues of the adult bird are compared with those of the chick, no matter what tissues are selected, it is found that those of the chick are coarser and less differentiated. In fact the elements forming the tissues of the embryo may be, relatively to the structures they form, so coarse that one might describe the embryo in its earliest stages as being built up of paving-stones and granite blocks. On this account the investigation of the embryos of the higher animals hardly ever requires a very great magnification, and if this be so it is manifest that there can be no preformation.

In spite of destructive criticism and constructive observation, preformation still possessed a few faithful adherents. Dutrochet (1837), the real formulator of the cell theory before Schleiden and Schwann, was an ovist but not a complete preformationist. The Batrachian egg before fecundation, he says, contains an animal already formed, but it is not yet a tadpole. It consists only of an alimentary sac or vesicle having a single opening, which becomes the anus of the adult. The mouth is formed subsequent to fecundation as a perforation at the other end of the gut. Thus the foetus pre-exists fecundation in the Batrachia. At that stage it is in fact a kind of polype, and this allows us to reconstruct in a general way the original form of the animal, which in principle should have been a simple vesicle, but which, becoming flattened on the globular vitellus, has taken, in

developing on it, the form of a two-layered cap. There can be no doubt that Dutrochet is here describing something he has actually seen, but it is equally certain, as Baudrimont and Martin Saint-Ange point out, that he must have been handling fertilized eggs which were already in a somewhat advanced state of development. In the same year Wagner, after a very careful examination of the microscopic structure of the unfertilized egg of the frog, could not find in it any traces of the foetus. He adds, very soundly, that only a very accurate analysis of the unfertilized egg and male sperm can give us any knowledge of the first stages of development, and without this knowledge further progress is impossible.

An admirable critical analysis of preformation was published by Dugès in 1839. One supposed proof of this doctrine he remarks, is that coagulation of the embryo by alcohol reveals parts which are not previously visible owing to their clearness and fluidity—a method, however, which may be employed with greater effect in support of epigenesis. Swammerdam, by the use of boiling water or alcohol, had found in the caterpillar all the parts of the future butterfly. Hence it was concluded that the perfect insect existed fully formed in the grub stage, and hence also the new-born grub was already surrounded by all the skins which it would successively throw off. This last assertion, says Dugès, which was at first only an inference, was afterwards treated as a fact, but since it is false, and the form of the butterfly only appears under the skin of the caterpillar before the last moult, and at the moment of metamorphosis, the bearing of this case is against the doctrine of preformation, and entirely in favour of epigenesis. Again, the innateness of germs (emboîtement) is supported by arguments based on probabilities which have never been demonstrated. This innateness can only rest on negative grounds, such as the difficulty of conceiving the formation of the germ and its parts by epigenesis—a difficulty which must of necessity disappear before the evidence of the facts. Dugès refers to the life history of the Aphis, which is considered to support preformation. In this animal there is a successive

déboîtement of female Aphis which, in virtue of the fecundation of the female which lays the first egg, gives birth to others even to the eleventh generation. From this it is concluded that the foetus must reside in the female, and that the male takes no part in its production. Dugès is unable to explain these facts except on the supposition, for which he admits he has no evidence, that the Aphis is hermaphrodite. His own view of the generative process is that the female provides the egg and nutritive materials, but for the rest all that can be said is that the two sexes intervene to a variable extent, but as a rule almost equally, in the constitution of the future animal. Their materials apparently mix and fuse in the vesicle of Purkinje [nucleus],[1] which would explain the structure of hybrids, where as a rule both parents play an equal part. He considers that the controversy as to whether the rudiments of the chick can be found in the egg before incubation may be due to some slight development whilst the egg is still in the oviduct of the hen.

It is not surprising to find in the romantic personality of Pouchet (1847) a belated but ardent ovist, and he thus deprives Blainville and Cuvier of the somewhat doubtful honour of being the last of that long line of philosophers. Pouchet claims that in many virgin eggs one may already perceive some simple structures which constitute the first rudiments of the foetus. He accepts the statements of Malpighi, Haller, and Spallanzani that the smallest parts of the foetus are present in the egg before it is shed and before fecundation. In the Mollusca, Pouchet professes to have found in the unfertilized egg a certain degree of organization, representing undoubtedly the beginnings of some of the viscera. The male, therefore, is not responsible for the foetus in the egg, but supplies only that vital impulse without which the eggs cannot develop, which explains any resemblance to the male parent the foetus may exhibit.

When Owen wrote the last volume of his work on Vertebrates (1868), he had abandoned his opposition to the principle of Organic Evolution, but still objected to the

[1] This is a remarkably shrewd guess.

name. He prefers to call it the 'derivative Origin of Species', and he admits that species tend to converge 'as time recedes to more simplified or generalized organizations'. He has, however, no place for the old evolution or preformation, and says that at the present day it is 'hardly worth the paper on which it is referred to'. Nevertheless preformation is logically inseparable from the doctrine of the origin of life by Special Creation, and if that is dropped preformation must go with it. He adds that preformation has now only historical interest, and he would not even have recalled it 'were it not that ghosts of "pre-existence" and "evolution" still haunt some chambers of the physiological mansion, and even exercise, to many, perhaps, an unsuspected sway over certain biological problems'. It seems almost incredible, but it is unhappily true, that the particular 'ghost' Owen had in mind was nothing less substantial than Virchow's doctrine *Omnis Cellula e Cellula* (1854), which Owen by some strange aberration regards as a modification of the old dogma of preformation, and contemptuously rejects it as the last rag of the pre-existence of germs. When it is remembered that Owen was writing in 1868, at which time the cell theory was some thirty years old, it is difficult to understand how the multiplication of cells by cell division could have been confused with the successive emergence of foetuses, all of which had been created at the beginning of the world and their numbers therefore irrevocably fixed.

Huxley (1878) ascribes the long life of the preformation doctrine to the lack of immediate successors to Wolff, and a period of over sixty years does in fact separate Wolff from Prévost and Dumas and von Baer. 'The school of Cuvier', says Huxley, 'was lamentably deficient in embryologists', and hence the task of proving 'the utter incompatibility of the hypothesis of evolution, as formulated by Bonnet and Haller, with easily demonstrable facts' was not completed until later. Huxley indulges in an unusually happy venture when he anticipates that future research will perhaps show that epigenesis is more superficial than essential, and that development is the expansion of a potential, but invisible, preformed

organism.[1] In this, Huxley exhibits greater insight than Oscar Hertwig, writing some fifteen years later, who considered that any theory of preformation threw back the mystery into an invisible world in which there was no possibility of attack by the investigation of the properties of visible structure. Such a doctrine, therefore, was unfruitful for research and offered no avenue for advance by inductive methods. That Huxley was nearer the truth than Hertwig now appears from the researches of Spemann and other experimental embryologists.

[1] Cf. Harvey and Oken, to whom this idea had previously occurred.

VI

EPIGENESIS

THE doctrine of epigenesis is usually associated with the name of Harvey, but it is impossible to read Aristotle's account of the development of the chick without realizing that Harvey adopted the idea direct from his authority. Aristotle puts to himself the question—do all the parts of the body, the heart, lung, liver, eye, and the rest, come into being together, or in succession? It is important to note that his answer to this question is based, not only on speculative probabilities, but also on actual observation. It is true that his epigenesis is of the order that the heart develops first (in the Vivipara from the menstrual blood), the internal parts before the external, and the anterior before the posterior—the succession being determined by the physiological requirements of the *adult*. Such an epigenetic series would certainly be suggested by a macroscopic study of the development of the chick. That there is no preformation, he says, 'is plain even to the senses, for some of the parts are clearly visible as already existing in the embryo while others are not; that it is not because of their being too small that they are not visible is clear, for the lung is of greater size than the heart, and yet appears later than the heart in the original development'. Neither does Aristotle believe that the earlier organs make the later ones, but that the latter 'come into being only *after* the others' and not by the agency of them. He also rejects preformation on philosophical grounds in the following passage:

'Yet again, if the whole animal or plant is formed from semen or seed, it is impossible that any part of it should exist ready made in the semen or seed, whether that part be able to make the other parts or no. For it is plain that, if it exists in it from the first, it was made by that which made the semen. But semen must be made first, and that is the function of the generating parent. So, then, it is not possible that any part should exist in it, and therefore it has not within itself that which makes the parts.'

Platt summarizes this paragraph as follows: 'If all the parts are made *by* the semen, it is evident that no part can exist *in* it from the first.' Aristotle is on solid ground in rejecting pre-existence on the strength of his observations on the chick, but his philosophical objection, depending as it does on a vital assumption for which there is no justification, must share the fate of all such efforts of the imagination.

The earliest writers on embryology after Aristotle are Coiter (1572), Aldrovandus (1600), Fabricius (1600, 1621), and Parisanus (1621). Coiter was the first to observe the blastoderm of the chick, which he describes on the first day as a white patch in the middle of the yolk,[1] but Aldrovandus perpetuates an ancient error in regarding the chalazae as the semen of the cock, and the chick as arising from them. The work of Fabricius is more detailed and ambitious. He uses the word ovum as applicable to the large meroblastic egg only, and not to the small egg with little or no yolk, which develops without an obvious yolk sac. The blastoderm of the newly-laid egg he names the *cicatricula*, because he regards it as the scar of the severed peduncle which originally connected the egg with the ovary, the egg being detached like an apple from its stalk. Hence according to Fabricius the blastoderm is meaningless and incidental, and may even be regarded as an actual blemish. He denies that the chalazae are the semen of the cock, but believes that from them, when fecundated by the male semen, the chick is built up, failing to observe that the chalazae do not occur in that part of the egg where the chick is produced. He saw the heart and mistook it for the body of the embryo, forgetting that he had already derived the chick from the chalazae, which were still to be observed in the egg. Fabricius asserts that the liver, heart, veins, arteries, lungs, and all abdominal organs are produced together, but the bones and framework are formed before the soft parts. The latter statement is not based on observation but on analogy, the building of the foetus being compared with the construction of houses and ships. Fabricius evidently cannot be regarded

[1] It is strange that Aristotle should have missed this, but he did.

as supporting either epigenesis or preformation, but preferred a system of his own. Parisanus gives us an original account of the development of the chick, and he is the first after Coiter to observe the blastoderm of the newly-laid egg, but he goes further than Coiter and anticipates Harvey in localizing the first appearance of the embryo in the blastoderm. This achievement, however, cannot be compared with Harvey's, for Parisanus interprets the cicatrix as the semen of the cock, or rather the white point in the middle of the cicatrix is the semen of the male, and represents the rudiments of the foetus. Parisanus refutes Fabricius' views on the chalazae, but does not himself recognize their function. Further, he appears to have mistaken the two eyes or bosses for the rudiments of the heart and liver.

Digby (1644) refers with admiration to 'that learned and exact searcher into nature, Doctor Harvey', and again 'the learned and ingenuous Doctor Harvey, who hath invented and teacheth that curious and excellent Doctrine of the circulation of the blood (as indeed, what secret of Nature can be hidden from so sharp a wit, when he applieth himself to penetrate into the bottom of it)'. Digby, like Aristotle, asks himself the question—'Are animals formed entirely at once or successively one part after another and in what order are the parts formed?' Having propounded this problem he leaves it unanswered, for he is not satisfied with pangenesis as then understood, and his own system is after all only a new version of that ancient doctrine.

It is a difficult and almost an invidious task to review Harvey's work on generation. His demonstration of the circulation of the blood gives him such an exalted position in British Science that we are almost tempted to forget his work on generation—in which the great man was making an heroic, and almost a pioneer, attempt to solve a problem which was insoluble by his generation, or for that matter, by ours. Hence it is inevitably a record of failure. The treatise was published in Latin by Pulleyn at London in 1651, and Pulleyn also arranged for an Elzevir edition to be issued simultaneously at Amsterdam, and in the same year and place two

further editions were printed. There are thus four editions bearing the date of 1651. The first English translation appeared at London in 1653. As Harvey died in 1657 it might appear that this lengthy dissertation was the fruit of his old age, but this is by no means the case. Ent refers to the long delay in publication, and John Aubrey describes Harvey as being concerned with generation at Oxford in 1642. Judging from references made by Harvey himself, he must have worked at generation *before* the publication of his work on the circulation in 1628, since the latter work has a passage which foreshadows the recapitulation doctrine in embryology, based, as he says, on numerous observations on the formation of the foetus. In the *De Generatione* itself Harvey refers to the raiding of his house in London during the Civil War, and the destruction of his papers on the generation of insects,[1] which papers must have been written before the forties, and in another passage he mentions observations on the development of the deer made in the year 1633, this work extending over a 'long series of years'. The composition of the treatise on generation therefore obviously covers a considerable period of Harvey's life, and he appears to have assembled his notes without making any attempt to collate or digest them.[2] This explains the endless repetitions and numerous contradictions which it contains, and hence the work is not so much a final and coherent theory of generation, as a history of the development of his opinions on this inscrutable topic.

There are several indications that Harvey's attitude towards research was a conservative one. He refused to recognize the lacteal vessels, for which, he says, there is no occasion in the chick, nor could he distinguish them in any bird. He ignored the compound microscope, which had been used with advantage as early as 1625, and only in three places does he mention the employment even of a simple magnifying glass. On the other hand, his own discovery of the circula-

[1] Harvey could not have inquired very deeply into the generation of insects, since he entirely failed to grasp the nature of their metamorphosis.

[2] Harvey at the time was an old man and may have left this task to his editor, Ent.

tion of the blood occupied the first place in his thoughts during the latter years of his life. The wonderful circulation of the blood first found by me, he says, is consented to almost by all. The heart beats after death. Blood is the fountain of life—the first to live and the last to die. The living principle first gleams forth in the blood. It is unquestionable and obvious to sense that the blood is first formed, and is therefore the generative principle of the embryo. The whole body is posthumous to the blood and appended to it. The blood lives of itself and supplies its own nourishment. These extracts may be regarded as the text on which Harvey's treatise on generation is largely founded.

Harvey has a very high opinion of Aristotle—in fact he speaks as if his own work were but a new edition of Aristotle, and he differs from him with misgivings and regrets. Whitman (1894) compares Harvey and Aristotle in the following words:

> 'Harvey's aphorism depends for its significance on the definition of the word ovum, but as defined by Harvey the whole idea shrinks to the doctrine of Aristotle, and nearly everything that is usually appealed to in his work in respect of epigenesis may be traced to Aristotle. Harvey's dictum is a vague generalization exceeding in no way what Aristotle had already maintained—in fact it may be regarded only as a fair summary of Aristotle's views and surpasses them only in metaphysical extravagance.'

This may seem a harsh criticism, but it is not wholly unjust. On the other side, however, we must not forget that the condition of embryological science in Harvey's time was such that he must receive the fullest recognition for the prophetic insight displayed in his views on the ovum and epigenesis. His demonstration that the cicatrix of the fowl's egg is the point where the future embryo will develop is of fundamental importance, seeing that it constitutes a first step towards a knowledge of the early stages of development. Also Harvey was a pioneer with Fabricius in the study of the early embryonic history of the Mammal, in which he obtained some noteworthy results.

It is now necessary to consider Harvey's views on the part

played by the ovum in development. The familiar expression *Omne vivum ex ovo* occurs nowhere in Harvey's writings. On the engraved title-page of two out of the four 1651 editions of the *De Generatione* is a figure of Jupiter holding in his hand an ovum, from which are emerging animals of all types, including man, and on the shell of the ovum itself are engraved the words *ex ovo omnia*.[1] In the two remaining 1651 editions these words are omitted. The heading of Chapter LXI (=LXII), however, is much more explicit than the words usually and wrongly attributed to Harvey. It reads: *Ovum esse primordium commune omnibus animalibus*. The history of the misquotation of Harvey's dictum is perhaps worth recording. Linnaeus, in his *Fundamenta Botanica* of 1736, uses the expression *Omne vivum ex ovo provenire datur*, but does not associate it with Harvey.[2] Wahlbom (1746), in commenting on this passage, says: *Harvaeus etiam, omne vivum ex ovo, olim exclamavit*. This appears to be the first use of the famous misquotation, and the first attribution of it to Harvey. It was not, however, adopted by other writers until later. The modern vogue of the error is perhaps due to Oken, in whose work *Die Zeugung* of 1805 there is a reference to Harvey's *Aufruf: Omne vivum ex ovo*. From this date the expression occurs very commonly in the literature, to the almost complète exclusion of the correct version. On the other hand the earliest references to Harvey's dictum up to about 1800, in all cases except Wahlbom, quote it correctly as *Ex ovo omnia*. Thus Garmann in 1672 refers to Harvey's 'daring' pronouncement *Omnia ex ovo*, Buffon first in 1749 and later in 1777 quotes Harvey's 'devise' and the 'false principle' *Omnia ex ovo*, and Parsons in 1752 mentions it as the 'standard opinion' of the 'immortal Harvey'. Ramström in 1759 introduces the slight variant *Omnia ex unico ovo*, not as Harvey's dictum, but as expressing his views; but after 1800 there are only a very few references to *Ex ovo omnia*,

[1] This is the correct order of the words, but the expression is often quoted as *Omnia ex ovo*.

[2] An anonymous reviewer in the *Annalen der Literatur und Kunst in dem österr. Kaiserthum*, 1812, who was familiar with this passage, was consequently led to attribute the dictum to Linnaeus.

such as Thomson of 1812 and Blainville of 1845, the inaccurate version having by this time entirely replaced it. Even as recently as 1925 the title of the Harveian oration was 'Some developments of Harvey's Doctrine *Omne vivum ex ovo*'.

Since the history of Harvey's dictum is the history of one of the fundamental principles of embryology, it is necessary to scrutinize closely the meaning which Harvey himself attached to it. *Quid sit Ovum*, What an egg is. This is the heading of one of Harvey's chapters, and it is manifest that whatever value his dictum possesses must depend on his treatment of this question. He has, in fact, several definitions, but they are all vague and indeterminate. The egg, he says, is a conception proceeding from the male and female, and endowed with the virtue of both. Hence it produces a foetus which resembles both parents.[1] The egg is the *terminus ex quo* and the *terminus ad quem*—it is the pivot round which the whole generation of the chick revolves. Harvey does not believe in preformation, which he says is not consistent with true generation, but he suggests that all parts of the embryo are present *potentially* in the egg, and he even uses the word pre-existence in this connexion. He was therefore the first embryologist to support pre-existence as distinct from predelineation in the ovum—a belief which has only been tested experimentally in modern times. Harvey attempts to explain generation by assuming the existence of a First Cause or Generative Principle, which has the power of initiating growth. This principle is inherent in certain diverse corporeal substances which exhibit intrinsic vitality, and are potential living organisms. Such substances are the eggs of animals, the seeds of plants, the conceptions [blastodermic vesicles] of Mammals, and the larvae and even the pupae of insects. Hence Harvey's 'ova' differ *structurally* from each other according to the type of animal life to be produced from them, and they only *agree* in possessing the generative

[1] This passage makes it difficult to explain Huxley's assertion that 'it is not expressly maintained by Harvey that the primordium oviforme proceeds from a living parent although this may be thought to be implied'.

FIG. 18. Engraved title of the Elzevir edition of Harvey's work on generation. This may be compared with the well-known title of the first London edition of the same date. Note the *ex ovo omnia* engraved on the egg

principle.) In this way he distinguishes between perfect and imperfect eggs. The former, such as the eggs of birds, are completed in the uterus before they are laid, and the latter, such as the eggs of fishes, are extruded prematurely and increase after they are laid. For example, the larva of a butterfly is an imperfect or creeping egg, and grows outside the body of the parent into a perfect egg or chrysalis, and by doing so reverts to the egg status. According to Harvey, therefore, the ovum is not itself a definite *primordium* exhibiting a common fundamental structure as understood to-day, but a widely varying secondary *product* of his primordial generative principle. Hence he is not consistent, since it is impossible to regard as a *common* beginning such a collection of odds and ends of developmental stages as are included under his term ovum. It is the *principle*, or the egg in a confused metaphysical sense, which is the common beginning, not a morphological ovum as conceived by the modern biologist. The dictum *ex ovo omnia*, whilst substantially true in the modern sense, is neither true nor false as employed by Harvey, since to him it has no definite or even intelligible meaning. Nevertheless it would be undiscerning to exclude Harvey from participation in the honour which belongs to those who established this dictum. All scientific principles are the products of evolution. As such they are subject to the laws of growth and modification, and their complete expansion may occupy centuries of human endeavour. Fifty years ago *ex ovo omnia* did not mean precisely what it means to-day, and Harvey's conception of it was not, and could not be, a modern one. Nevertheless it was Harvey who gave the initial impetus to that long series of researches, which discovered in his dictum a profound truth of which he himself was only dimly conscious.[1]

Harvey has no difficulty in overthrowing the interpretation of the cicatricula [blastoderm] of the fowl's egg adopted by Fabricius. It is, he says, the rudiment of the embryo. It is the spot where the first spark of the vital principle is

[1] The opinion of a youthful critic that 'Harvey did not mean "omnia" and did not know what "ovo" was' briefly summarizes the situation.

kindled. His assumptions that it is itself formed from the albumen,[1] and gives rise first to the blood and pulsating vesicle or punctum saliens, are of course erroneous, but apart from this Harvey may claim, as he does, to have been the first[2] to *demonstrate* the real nature of the cicatricula, although Parisanus had already suggested a somewhat similar interpretation. Harvey is very sound in his observations on the chalazae of the bird's egg. In spite of the fact that Aristotle had refused to concede any reproductive powers to these structures, the traditional view that they represented the semen of the cock was generally accepted. Fabricius, it is true, had denied this, but his own theory was even more misleading, and Harvey, in disposing of it, points out that the chalazae are present in the eggs of all birds, whether prolific or sterile, that they are still to be found unchanged after the chick has developed, and that the chick arises at a point remote from the chalazae. His own belief is that the chalazae perform a mechanical office only, and are responsible for keeping the yolk sphere in the centre of the egg and the right side up, which is in accord with modern beliefs.[3]

Time after time Harvey returns to his dictum that all life proceeds from eggs. He asserts boldly that 'all animals whatever, even viviparous also, nay Man himself to be made of an egge: and that the first conceptions of all living creatures which bring forth young are certain egges. . . . The history therefore of egges is most spacious, because it yields an insight into all Kinde of generation'. Yet notwithstanding his adhesion to this general principle, he cannot bring himself to reject outright the doctrine of spontaneous generation. 'The earth', he says, 'also produceth many things of its own accord, without any seed.' He then proceeds to discount this statement by claiming that some seeds are so small as to be invisible, and are scattered and

[1] Aristotle states that the chick is developed from the albumen but is afterwards nourished by the yolk, in which he differs from Hippocrates and other Greek philosophers.

[2] Highmore had independently reached the same conclusion, and published it a few weeks after the appearance of Harvey's work.

[3] Boyle (1690) gives a similar interpretation of the chalazae.

dispersed by the wind, so that the animals which they produce are supposed to arise spontaneously because their ova cannot be found. Later still he again accepts the possibility that some animals may arise spontaneously from putrefactions. His attitude towards spontaneous generation therefore is one of qualified acceptance.

The principle of epigenesis, which derives the embryo from an apparently undifferentiated and homogeneous egg by a gradual process of differentiation and growth, is indissolubly connected with the name of Harvey. He appears to have been the first to coin the term, and the form of it he first uses is *per epigenesin*, but in the English translation of 1653 the word epigenesis itself is employed. Harvey distinguishes two types of development in animals, which types he says are very different. (1) By *metamorphosis*. (All parts are formed *simultaneously* out of material previously concocted, so that a perfect animal is born suddenly as in an insect emerging from a chrysalis. Metamorphosis may be compared with the impression of a seal, or adjustment in a mould—the whole pre-existent raw material being given a form in one brief operation. Hence all parts are simultaneously constituted and embodied, and in consequence a perfect animal is born.) Harvey therefore did not apply the principle of epigenesis to all animals, but deliberately excluded those arising by metamorphosis. His views on the metamorphosis of insects were severely and justly criticized by Swammerdam. Harvey tells us that he had worked on the generation of insects, and had, in fact, prepared a treatise on this subject, but nevertheless he failed to observe that the development of an insect was really gradual and only apparently cataclysmic. (2) By *epigenesis*. One part is made before another, and development proceeds as the result of successive accretions. The parts so developed increase in size and alter in form. Such animals start from a central point or nucleus (such as the cicatricula of the fowl's egg), and from this nucleus the animal arises part after part in a definite sequence. 'It is plain that the chicken is built by epigenesis, or the additament of parts budding one out of another.'

Epigenesis, he justly observes, is more properly called generation than metamorphosis.

When all other resources fail and Harvey is sorely puzzled, he falls back on the Deity: 'But as in the greater world, we say, *Jovis omnia plena*, all things are full of the Deity, so also in the little edifice of a chicken, and all its actions and operations, *Digitus Dei*, the finger of God, or the God of Nature, doth reveal Himself.' There is no occasion to review Harvey's theory of metamorphosis, which is manifestly wide of the mark, but it is necessary to see whether the part of his system which on the face of it is sound, and with which his name has always been associated, will bear a searching examination. Whether Harvey's conception of epigenesis is to be justified, or whether it is to yield but the nucleus of the truth, his views on organogeny must decide. When dealing with this important matter he becomes very metaphysical, and that is always a bad sign. In the case of the chick, he says, no part whatever of the embryo is present on the third or fourth day except the heart and its vessels.[1] Therefore the first part of the embryo to be laid down is the blood vascular system. 'I am fully satisfied', he says, 'that the blood hath a being before any other part of the body besides, and is the elder brother to all other parts of the foetus, and that from it both the matter out of which the foetus is constituted, as also the aliment by which it is supplied, is derived, and it is (if anything be) the first genital particle.' After the blood system has been initiated the body appears in the form of a little maggot or worm, which wraps itself round the heart and vessels so as to enclose them. This worm then proceeds to differentiate into two regions—an anterior and a posterior. At first the anterior region develops faster than the posterior, but finally the latter overtakes and passes it. The eyes appear first, then the brain vesicles, and later the sides of the body with the ribs and the

[1] Aristotle states that traces of the embryo appear after the egg has been incubated three days and nights. He saw the heart beating in the living embryo and the vessels associated with it. He gives a good description of the embryo and its vessels at the fifth day of incubation.

organs of locomotion—wings and legs. The viscera come last, after the trunk has been formed, and the gut, liver, lungs, and urogenital organs all appear simultaneously and take their origin from the blood-vessels, to which they are attached 'like fungi growing on the bark of trees'. When one compares this with the masterly analysis of the organogeny of the chick published some twenty years later by Malpighi, it is difficult to concede that Harvey had more than a very shadowy conception of what development by epigenesis actually means. It is easy to see where he went astray. He accepted too much from Aristotle, and expected his own unassisted eye to suffice, in matters which could only have been revealed by the miscroscope.

Harvey only briefly notices the theory of pangenesis—probably the most ancient theory of generation. He opposes it as incompatible with epigenesis. The latter theory, he says, assumes that out of one body of a homogeneous nature diverse and contrary bodies arise, or, in other words, there is a segregation, or disgregation as he calls it, of a homogeneous substance, whereas in pangenesis there is an assemblage or concentration of heterogeneous particles.

Notwithstanding the powerful combination of Aristotle and Harvey, epigenesis found no supporters. Everard (1661), who bases his work largely on Harvey, opposes epigenesis none the less, holding that the foetus of the rabbit is formed instantaneously as in a mould, and that when one part is visible, such as the heart, all other parts are present also, although they may escape the eye. De Graaf (1672) does not discuss epigenesis, but his own observations are not inconsistent with it. In the rabbit he does not find a definitely formed embryo before the tenth day after coitus, when it appears like a 'vermiculus' attached to the placenta by a thin cord. By the twelfth day, however, the embryo has become conspicuous, and the main divisions of the body, such as the head, neck, and trunk with limbs and tail, can now be observed. The objection to epigenesis urged by Perrault (1680) is that if the egg consists of homogeneous matter, as is presumed on this hypothesis, it can only develop into

a foetus by a miracle which would surpass every other phenomenon in the world.

A well-known supporter of epigenesis, and be it noted, before Wolff, is Swedenborg (1740). (In the formation of the mammalian foetus and also in the chick, he says, the several parts are produced successively in their own proper order, and there is no effigy in miniature in the germ, no trace of the future body, and no prototype which is simply expanded.) All parts must come into existence one after another, organ after organ [seminis extensio]. Not a shadow of the future body is at first apparent. 'If we glance through the entire process of formation, as unfolded and described by Malpighi and Lancisi, we shall not find any two members developed simultaneously, nor the effigy of any member in its smallest form to be the same with that of its largest and most expanded form; nor anything simply swelling and enlarging and preserving the same shape throughout its progression.' According to Swedenborg, the embryo passes through four stages or diversities of state during development: (1) in virtue of the existence of a certain formative force, power, substance, or spirituous fluid, which exists throughout life, a thread is drawn from the first living particle, and the central nervous system is laid down; (2) the purer or white or spirituous blood, which arises before the red blood is developed, is responsible for the production of the heart and larger vessels in their simplest form; (3) red blood appears, the motion of the heart begins, and the formation of the lungs is thereby initiated; (4) period of birth or hatching, when the lungs begin to function. In a later work, written *c.* 1744 but not published until 1849, Swedenborg again favours epigenesis. The central nervous system, he says, is formed first, and constitutes the carina of the foetus. This is the highest region of the body, the other parts being formed in succession under it, i. e. inferior and partly external to it. They 'take their origin from the brain as their Olympian heights'. Swedenborg was a close student of the literature of biology, and it would have been possible by making use of Malpighi's observations and discarding his

opinions to have compiled a much more convincing system of epigenesis.

Boerhaave (1744), who was disposed rather to favour animalculism, has yet something to say for epigenesis. According to him all embryos are at first no more than worms, possessing, it is true, certain important structures such as the brain, spinal cord, and eyes, but only later developing the heart, liver, and lungs. These latter organs are not present in the early embryo, although it is provided with the matter from which they are formed. Further, the organs themselves when they first appear are simple in structure, and hence have to undergo progressive differentiation, e.g. the heart is at first a twisted canal, and only later becomes transformed into a four-chambered heart. Boerhaave's views thus represent a compromise between epigenesis and preformation. Haller's early belief in epigenesis and his conversion to preformation have already been alluded to. His reply to Wolff in 1766 is far from convincing. He seems to be shaken, and speaks highly of Wolff. He contents himself with repeating his statements that the blastoderm [of the modern embryologist] is present in the unincubated egg, and that its vessels are not visible because they are not yet filled and distended with red blood. He does not join issue with Wolff on the solid ground of observation, but draws up a long list of questions, based on *a priori* abstractions, which he seems to think Wolff will find it impossible to answer.

The doctrine of pangenesis may on occasion be regarded as complementary to epigenesis, since it attempts to explain the origin of the particles of the ovum which differentiate out as the foetus, and moreover it is definitely antagonistic to emboîtement. Epigenesis is concerned with the development of the embryo from the fertilized ovum, but pangenesis undertakes to explain the origin of the ovum itself. Maupertuis (1744) believes in a combination of pangenesis and epigenesis, each sex contributing equally to the formation of the foetus, but he will not allow the egg and sperm to take any definite part in generation, which is effected by the mixture of the male and female semen in the mass. He

admits that his system by no means explains all the facts, and regards it only as a step towards the ultimate solution of the problem, remarking complacently that those who are content to follow truth from afar, and to see it only dimly, may nevertheless succeed better than those who, in spite of greater proximity, see things that are not there.

The most celebrated protagonist of epigenesis is Wolff (1759), but Malpighi should be honoured as the real founder of the doctrine in modern times, notwithstanding his own belief in preformation. The account of the embryology of the chick given by Malpighi is admirably adapted to illustrate development by epigenesis, and it is difficult to understand the genius of a man who could accurately trace the development and emergence of the heart, step by step, through a diversity of stages, and yet believe that the *complete* organ was there all the time. Wolff takes his stand on the contention that the building up of the chick during ontogeny can be studied under the microscope, and that when it is so studied there is no evidence of an encapsuled foetus. Hence there is no enlargement of a pre-existing miniature, but a continuous growth accompanied by the gradual assumption of a complex form. That Wolff did not succeed in observing the first manifestations of development does not affect his argument that the earliest phases which *are* observable are inconsistent with the belief in the expansion of a preformed organism. He studied all the organs of the body with the same result. Nature was in fact able to produce an organism out of formless material simply by the force, which he named the *Vis essentialis*, inherent in that material. The first system to arise and to take definite shape is the nervous system. This is followed by the muscles, the blood-vessels, and finally by the alimentary canal, each system being a complete and self-contained whole, and arising at the stage appropriate to itself. Wolff energetically denies Haller's contention that the yolk membranes [blastoderm], which he says are two in number, exist before incubation. They are new formations, and only come into existence after incubation. Consequently the continuity of

these membranes with the foetus does not prove that the foetus existed before incubation when the yolk was still in the body of the parent. In a later work on the development of the gut Wolff shows that the digestive system also arises by epigenesis, and that the gut is at first a straight tube without convolutions. Histological development, in fact, is a continuous and progressive differentiation of an originally homogeneous tissue. Wolff's conclusions, however, made little headway. The work of a young man, expressed in an inaugural dissertation, is not calculated to attract attention. Epigenesis had never been popular, and the noisy and confident disputation of the ovists and animalculists had almost completely obscured it. But from about 1740 epigenesis began to acquire momentum, and to attract the attention of the younger generation. Nevertheless, some seventy years after the publication of Wolff's dissertation, we find Cuvier, in discussing the development of the vascular system as described by Wolff, confessing himself unable to understand how the geography of this system can be preserved unless the scheme is to some extent pre-ordained, nor will he admit that Wolff's description of the development of the gut favours epigenesis. Sachs severely criticizes Wolff for his 'feeble' arguments against the theory of preformation. A correct appreciation of the sexual act in plants, and of the phenomena of hybridization, are in themselves, he says, a sufficient and final refutation of preformation, but Wolff failed entirely 'to perceive what it is which is essential and peculiar in the sexual act'. But this is to attack the problem from a new angle, and, important as this angle may be, it is hardly permissible to condemn Wolff for leaving something for his successors to discover. By directing attention to two points: (1) that in the unincubated egg no miniature foetus can be demonstrated; and (2) that the presence of such a miniature is unnecessary, since the formation of the embryo can be fully accounted for without it, Wolff performed a service to embryology of incalculable value. According to O. Hertwig, Wolff's dissertation was unconvincing at the time owing to the undeveloped condition of the methods of

biological research, with the result that more importance was attached to abstract reasoning than to observation.

Bonnet (1762), after referring to the controversy between Wolff and Haller as to whether or not the vascular membrane of the yolk was present in the unfertilized egg, and naturally deciding to support Haller, proceeds to criticize Wolff's Essential Force. All force, says the philosophic Bonnet, is indeterminate and cannot of itself produce specific effects, or in other words it presupposes the existence of the mechanism which it activates. If, therefore, there is nothing preformed in the matter which the essential force is supposed to organize, how can that force produce, let us say, an animal instead of a plant, a particular kind of animal, and a special set of organs of the proportions and arrangement appropriate to that animal? There is some wisdom in this criticism, and Wolff's Essential Force, like the many other forces which have been invoked to explain generation, is nothing but a confession of ignorance. The fallacy of Bonnet's argument is not the form of it, but the rather more subtle one of assuming that the machinery to be energized can only be the machinery of a visible preformation. It will be remembered that Bonnet's pre-occupation with his beloved theory is such that, like Malpighi, the obvious and admitted facts of development cannot prevail against him. He swallows with avidity, however, any scrap of evidence in its favour. In 1771 he writes to Spallanzani to compliment him on his work on Infusions, and exclaims: 'Behold the poor epigenesist reduced to an impalpable powder. You have pulverised no less his friend Buffon.' A more defensible criticism of epigenesis, which Bonnet advanced in 1764, is that it is mechanical,[1] and he cannot understand how the brain, heart, and other organs of the body can be produced by the laws of mechanics, seeing that they are all mutually dependent, and therefore cannot exist separately. The body of an animal is an organic whole, and must be brought into existence as a whole, and not piecemeal.

'Look', he says to those who favour 'mechanical' explanations, 'at

[1] Architectural would better express his meaning.

the wonders which the graver of the celebrated Lyonet has illuminated. Can you behold without profound astonishment those four thousand muscles employed in the make-up of a caterpillar and their admirable co-ordination, and again those tracheae no less wonderful? Is it not obvious that a whole so marvellously and harmoniously made, and so essentially unified, cannot have been assembled like the parts of a watch, or by the mustering of an infinity of diverse molecules united by successive apposition? You must admit, I hope, that such a whole bears the indelible stamp of a work accomplished at a single stroke. To what purpose do we torture our minds by seeking mechanical solutions which do not meet the case, when there are decisive facts which seem to lead us as by the hand to the pre-existence of germs?'

Bonnet would have described this as preferring the single miracle of the Creation to the endless miracles of epigenesis.

Voltaire (1767) mentions Harvey's treatise on generation. The celebrated Harvey, he says, who was the first to demonstrate the circulation, was the very person to discover the secret of generation. As the result of Harvey's work 'il fut établi dans toute l'Europe que nous venons d'un œuf', and, he adds on his own behalf, 'notre globe est un grand œuf qui contient tous les autres'. In 1777 Voltaire again refers to 'Aryvhé' on generation, and quotes his dictum as 'tout vient d'un œuf'. He does not, however, discuss his views on epigenesis. Blumenbach (1780) played no small part in the ultimate revival of epigenesis, but his efforts were directed rather towards the destruction of preformation than the establishment of its rival. There is no doubt that his caustic and humorous criticism, which enjoyed a considerable vogue, hastened the reaction against preformation, which was at that time represented only by the dwindling supporters of ovism. Blumenbach himself is by no means a typical epigenesist, and his system has no place for egg or sperm. Both parents, he says, are equally concerned in generation, but the seminal matter is unorganized. At the appropriate moment it becomes controlled by an inherent vital stimulus, which he names the *Nisus Formativus*, and this continues to act throughout the whole life of the animal, causing it to assume and maintain its proper form, and restore it when damaged.

The Nisus, he observes, must not be confused with the normal properties of matter such as irritability and contractility, but it is the underlying motive force of nutrition, growth, and generation. He admits that he knows nothing of the ultimate nature of this agent, which is known only by its effects. Blumenbach's Nisus is little different from the formative principles of the earlier writers and the vital force of the later ones, and like them it can only be regarded as the symbol of ignorance. Epigenesis is claimed to be supported by the development of the chick, in the early stages of which there is not even the most distant resemblance to a bird. The Nisus Formativus was not favourably received. Bostock (1830) observes:

'It will be sufficient to remark concerning it, that it affords an instance of that incorrect method of introducing new terms into Science, which as they do not express the generalization of facts, throw no real light upon the subject in question, and which must therefore retard the progress of knowledge, by inducing the mind to remain satisfied with the acquisition of a new language, without having acquired any new ideas.'

The admirable account of the embryology of the chick written by John Hunter between 1773 and 1780, but not published until 1840, contains the most detailed and accurate figures of that much studied animal which had up to his time been published. The manuscript is in the library of the Royal College of Surgeons, and was not one of those removed from the College and destroyed by Home. The plates, which are very beautiful, were drawn by W. Bell, and one of them is dated 1779. The chick, says Hunter, is formed in the cicatricula of the egg, 'but before incubation no traces of the embryo can be discovered, there being no difference between this part that is impregnated and one not impregnated'. This naturally is a negative conclusion which, owing to the smallness of the parts, may not correspond with the actual facts. Hunter mentions three principles of development: (1) preformation; (2) metamorphosis; (3) a modified form of epigenesis, in which the parts are present at the beginning, but are altered in form and function as development pro-

ceeds. He thinks he sees all these principles in operation, but not in the same animal, or in the same orders of animals. Hunter was notoriously ignorant of the work of his predecessors and contemporaries, and he says nothing of the spermatozoa or of the theories of generation in vogue at his time. It is surprising that Goethe (1817) should never have declared himself for epigenesis as against preformation. He considers that more investigation is necessary before either of these terms conveys anything definite, and therefore postpones coming to a decision.

The important researches of Prévost and Dumas and von Baer between 1824 and 1828 no longer left any room for doubt, and from this time epigenesis was accepted as the fundamental law of development. The former authors, whilst adopting views much less sound than von Baer's, maintain that the spinal cord or its rudiment always appears well before the other organs, and it is around this centre of crystallization that the various systems are *successively* built up.[1] They are, further, greatly impressed by the extraordinary resemblance between the early embryos of the mammal and bird, which is so great, they say, that the most experienced observer is unable to distinguish in any certain manner the foetus of the dog or rabbit from that of the chick or duck of corresponding age. This was quite a novel point, and although it was pressed too far, its bearing against preformation is manifest.[2] Dumas solus publishes his final and considered views in 1827. He first quotes from a letter received from his collaborator Prévost, in which the latter asserts that the cicatricula of the fowl's egg must be regarded as the female agent in generation, and it is there that the first rudiment of the foetus must be sought. It appears as a median shaft or axis in the cicatricula, and it is formed by the spermatozoon, which, however, is later destroyed, and does not remain as an integral part of the foetus. Prévost

[1] Cf. Rolando (1823), who had already reached a similar conclusion.

[2] This recalls the well-known incident in which von Baer himself figured. He possessed two small embryos in spirit, from which the labels were missing, and he was unable to decide whether they were very young lizards, birds, or mammals.

adds that the facts of development which he has observed are not favourable to the theory of emboîtement. The foetus is the result of the awakening effect of the sperm on the germinal spot of the egg, but neither the sperm nor the egg forms a part of the embryo which afterwards develops. They are responsible for the first only of a series of changes which result in the gradual formation of the foetus. Dumas now returns to his own conclusions. The sperm, he says, having penetrated bodily into the ovum, forms first the primitive streak [of current terminology] and then the rudiment of the nervous system, all the other organs of the foetus being formed by the remainder of the germinal disk. Thus both parents participate in the building up of the embryo, and the resemblance of offspring to their parents is explained. The old theory of emboîtement can no longer be maintained in the face of the facts of development. It is unfortunate that hasty speculation diminishes the value of the excellent observational work carried out by Prévost and Dumas, and it is little excuse to urge that they were misled by a supposed resemblance between the primitive streak and the spermatozoon, since there is here a difference in dimensions too considerable to be explained or ignored. It was also pointed out at the time by Dugès that an Invertebrate with a concentrated, as opposed to a linear, nervous system may yet produce sperms of the Vertebrate type.

Serres (1827), who supported epigenesis, attacks the preformation doctrine from a new angle. An organ, he says, does not necessarily attain its mature form by simple expansion and growth as assumed by the evolutionists. It may even pass through stages inconsistent with its final structure. For example, the human kidney begins as a number of 'little kidneys', which fuse to form the definitive kidney. A similar course is followed by other organs, which may be built up by the formation of successive new layers, such as the spinal cord, the bones, and the gut. This is epigenesis but not preformation. Immediately before von Baer (1828) there was a sudden revival of the belief in epigenesis, but it was von Baer himself who clinched that belief, and made it impossible

for descriptive embryology ever to go back on it.[1] But creeds die hard, and the old controversy was still maintained here and there on the old philosophical basis. Thus Bostock (1830) prefers epigenesis on grounds of probability, and expresses himself as follows: 'Although the hypothesis of epigenesis does not afford us any satisfactory explanation of the generative function, it is the only view of the subject which we can take, that does not involve some position, either absolutely contradictory to the laws of Nature, or, which appears in the highest degree improbable, if not altogether beyond our conception.' On the other hand Laurillard in his Éloge of Cuvier (1833) remarks that, not seeing in Nature any force capable of producing organization, Cuvier adopted the system of the pre-existence of germs—not the pre-existence of beings fully formed, since it is very evident that it is only by successive developments that animals acquire their form, but the pre-existence of the *radical de l'être*, which existed before the materialized embryo, and certainly goes back, according to the beautiful observations of Bonnet, for many generations. This is, however, hardly a correct description of Cuvier's position. It is true that in his later years he had expressed vague and indefinite opinions on the relative merits of preformation and epigenesis, but at other times he made it quite clear that a literal preformation was an acceptable doctrine.

[1] Von Baer's observations and opinions have been fully discussed by many writers. Cf. particularly Huxley in Taylor's *Scientific Memoirs*, 1853, and Russell, 1916.

VII

EARLY THEORIES OF FERTILIZATION AND DEVELOPMENT

FABRICIUS (1600, 1621) is the first modern author to propound a reasoned scheme of generation. Animals, he says, are produced spontaneously from putrefactions, from eggs in the oviparous animals and from seminal fluid in the Vivipara. He distinguishes between intra-uterine and external generation. In the former, the seminal fluid and blood give rise to the foetus, and in the latter, the ovum. He denies that the spermatic fluid of the cock reaches the oviduct or forms any part of the chick. It fertilizes the egg not by contact or in any material way, but by some subtle radiating influence. The chalazae are not the semen of the cock, but from them when fecundated by the male semen the chick is built up. Hence the chick is formed neither from the yolk nor the albumen, both of which become vascularized and are purely nutritive, diminishing as the embryo feeds on them during growth. The emanation which proceeds from the male semen modifies first the essential constitution of the chalazae, then induces a developmental phase, and finally a power of growth. He illustrates the pervasive effect of the semen by drawing attention to the phenomena of castration, where a purely local injury results in modifications in all parts of the body. Harvey agrees with Fabricius' views on fertilization, but is easily able to refute his statements as to the function of the chalazae. Fabricius discovered the Bursa Fabricii of birds, which is named after him. He considered it to be a receptaculum seminis, and to be able to store the semen of the cock for an entire year. Harvey pointed out that it was present in the male also, and that no spermatic fluid could be found in it. Attempts to locate the semen of the cock in the egg have been frequently made, and it is a popular delusion even to-day to discover it in the chalazae. Parisanus (1621), who observed the early stages of the development of the chick, but misinterpreted

them, prefers to find the male semen in the cicatricula of the newly-laid egg. Digby (1644) is an early critic of pangenesis. He says that according to some it is manifest that the living creature is produced from the superfluous nourishment which proceeds from all parts of the body, and may be said to embrace in some sort the perfection of the whole living creature. These substances under suitable conditions are assembled in conformity with the posture and disposition of the parts from which they are derived, and hence by growth do produce a creature similar to that from which they came. The evidence for this hypothesis was illustrated by the following example. A cat had its tail cut off when it was very young. Afterwards having kittens, it was found that half of them were tailless and the other half had tails of the ordinary type, the inference being that as one parent had a tail it could supply half the progeny with tails but no more. Digby himself, however, does not favour pangenesis. He cannot conceive the mechanism by which particles are collected from all parts of the body, especially from the outlying parts. He says: 'It is impossible every little part of the whole body should remit something impregnated and imbued with the nature of it.' He believes in spontaneous generation—vermin from corruptions, caterpillars from decaying sticks, and eels from mud, which is naturally impossible if animals are engendered by any process of pangenesis. Further, metamorphosis cannot be explained in this way, for how could the particles of a caterpillar be assembled to form a moth? [1] His own explanation is that generation is akin to digestion and assimilation. If the parts of the body can be augmented by digestion, why may not a corresponding process account for their generation in the first place? He supposes that the superfluous nourishment is drained off and concentrated in a place fit for it, and that there it is worked up into an embryo. This differs from pangenesis,

[1] Aristotle's ingenious and searching criticism of pangenesis may be summarized here. He points out that children may inherit characters from their grandparents, and may resemble their parents in the *dead* parts of the body, such as hair and nails, and again in functional matters, such as voice and mode of walking.

first in the nature of the material made use of [i.e. superfluous nourishment], and second, in that this material is not drawn from *all* parts of the body. The nourishment or 'homogeneal compounded substance' is changed by 'outward agents' into a second quite different and less homogeneal substance, which in its turn is changed into a third still less homogeneal, and in this way by successive mutations a complex organism is produced. This speculation, which cannot pretend to have any relation to the facts of development, may be described as a philosophic form of epigenesis. Although Digby does not derive his generative substance from all parts of the body, he believes that the body generally is capable of affecting it by the intermediation of the blood stream, which keeps the raw material of generation *en rapport* with the organism as a whole, and hence explains the non-inheritance of the cat's tails already mentioned. The blood has 'in it the virtues of all the parts it hath often run through'.

Harvey (1651) is on difficult ground in the section of his work which deals with the embryonic history of the Mammal (*Cervus*). He recognizes that the development of the Mammal is essentially the same as that of the chick, the only difference being in the relations of the foetus to the parent. He, however, takes up the unusual position of regarding the mammalian ovary as a kind of venous plexus, the object of which is to concoct a fluid for lubricating the parts. He holds that the ovaries do not exhibit any changes during the period of sexual activity, nor are they of any use in generation. He thus fails to recognize that the ovary of the bird and the mammal are homologous structures. After repeated dissections both of the bird and mammal, Harvey could not discover any trace of the male semen in the female genital ducts, and he therefore agrees with Fabricius that the male semen never reaches the seat of generation in any animal. He is very emphatic on this point, and returns to it again and again. The male semen contributes neither form nor matter to the egg, but only that by which the egg becomes fertile and fit to engender an embryo. He suspects that this

is done by a kind of contagion, effluvium, intangible penetration, seminal aura or essence, the male semen affecting even the body of the female in such a way that eggs which have still to be produced, and do not yet exist in the ovary, may yet be made fertile. Having performed this subtle office, the male semen either escapes from the body, or is dissolved, or is turned into vapour and vanishes. This lapse naturally affects Harvey's views on the nature of conception, which he endeavours to explain by identifying the behaviour of the uterus with that of the brain, a uterine conception being directly comparable with a mental one. But he admits, and even emphasizes, his ignorance of the mechanism of fecundation. Harvey's knowledge of the mammalian blastocyst, or ovum as he calls it, begins at about the second month, and this is what he describes as the first stage. He justifies the application of the term ovum to this stage, and follows Aristotle in regarding it as an egg which does not develop a shell. For a whole month or more, he says, nothing is to be found in the uterus after coition. He discovers the peculiar form of the blastocyst in the deer—its curious elongated shape, and extension into *both* horns of the uterus. He does not distinguish between the chorion, allantois, and yolk sac, but links them all together as the chorion. Fabricius was more accurate than Harvey in his interpretation of the foetal membranes. Harvey failed to recognize the allantois as a separate structure, and in fact will hardly admit its existence. He acknowledges only the chorion and the amnion—the former enclosing the whole conception and extending into both horns of the uterus, and the latter confined to the embryo, for which it forms a protective envelope restricted to one horn of the uterus. He describes identical twins enclosed in a common chorion or ovum, but each having its own amnion. In the mammalian ovum the vascular system is said to develop first, and the worm or body afterwards, as in the chick.

The cotyledonary placenta of the ruminant, which is mentioned by Aristotle, and described and figured by Fabricius, was first correctly interpreted by Harvey, who compares it

anatomically and physiologically with the compact placenta or uterine cake of man. But Harvey's views on the placenta underwent so much change during his lifetime that their final form is not easy to determine. He states correctly, against Fabricius, that there is no continuity between foetal and maternal blood-vessels, and hence the foetus is not *directly* nourished by the blood of the mother. In proof of this he cites cases of Caesarian section, when the foetus was lively, and its arteries pulsating, after its mother was dead and stiff. The foetus therefore has a life and vascular system of its own independent of that of the parent. Harvey now proceeds to nullify all this by the following extraordinary speculation. He states that the vessels passing between the parent and the placenta are mostly arteries. The placenta is a kind of uterine mamma or neutral zone between arteries and veins, and itself contains little or no blood. It prepares a milk-like albuminous aliment which is taken up by the foetal vessels of the placenta, almost all the latter being veins, and is carred to the foetus. This is surely an amazing doctrine to come from the discoverer of the circulation of the blood, since it implies that the blood does not circulate in the placenta or even in the foetus. It is, however, flatly and happily contradicted by a later passage, in which Harvey correctly describes blood carried by the arteries of the foetus to the placenta, and the return of the same blood plus nutrient matter absorbed in the placenta to the foetus by means of the veins. The contradiction is explained, but not of course justified, on the assumption that the first condition was believed by Harvey to obtain in the early, and the second in the later embryo.

The interesting little work on generation published by Highmore is dated May 15th, 1651. In a letter to Slegel dated March 26th, 1651, Harvey refers to his own work on generation as having just been published, and it therefore preceded Highmore's by a few weeks. Highmore refers to Harvey's book, an observation in which had been described to him by Sir Kenelm Digby, but apparently he had not seen the treatise himself. Highmore's theory of generation

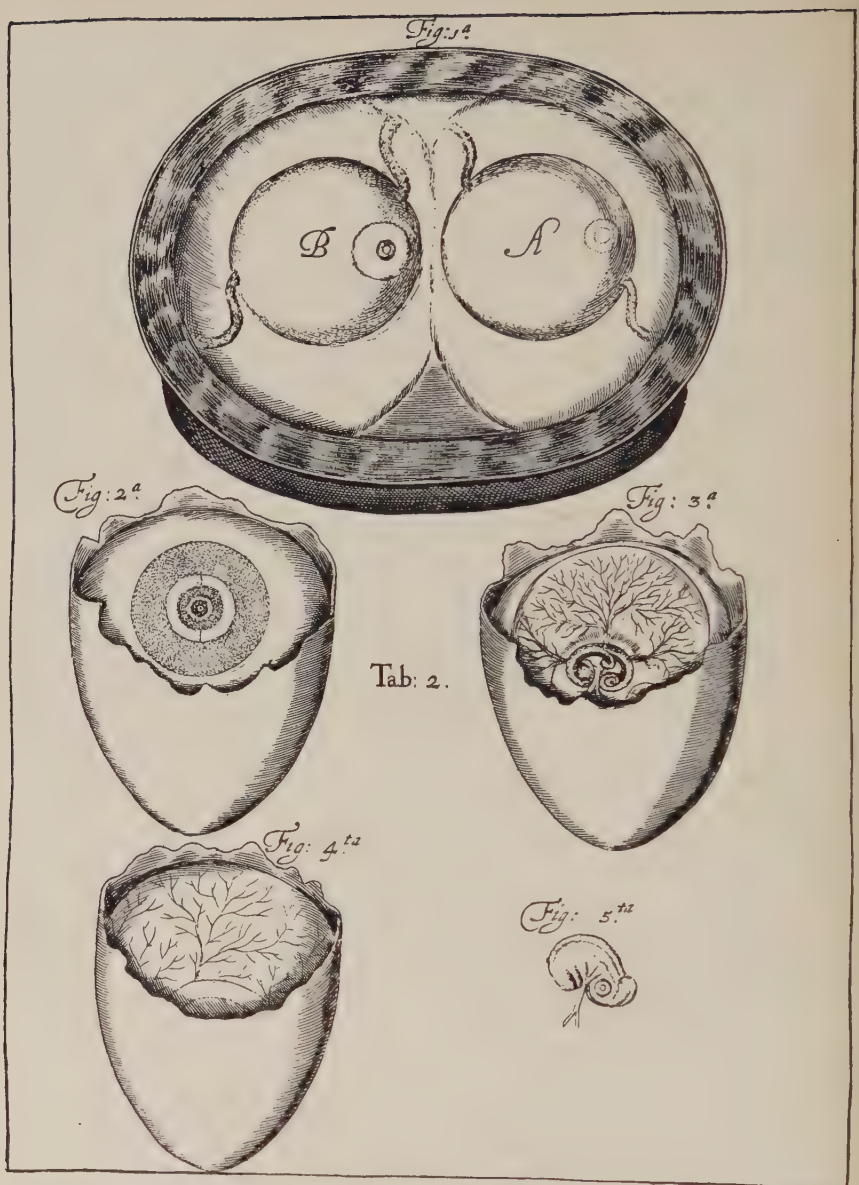

FIG. 19. Highmore's figures of the development of the chick in the first days of incubation. *A*, the unincubated egg with cicatricula; *B*, egg incubated for one day —cicatricula larger and more defined; *2*, after two days' incubation—cicatricula greatly enlarged and showing the opaque and pellucid areas; *3*, after four days', and *4* and *5*, after five days' incubation

is that the raw material thereof, capable of building up a complete foetus, is present as a very subtle quintessence or seminal principle in the blood stream, and hence in due course it is carried to the reproductive glands, where representative atoms are abstracted from the blood and worked up into the seed. Thus the genital glands collect atoms corresponding to every part of the body, which atoms, instead of being employed in building up the soma generally, are diverted to another office, and undergo concentration in the gonad into the germ. Consequently the germ represents the *substance* of the whole body, but not its visible form. This is pure pangenesis, and in fact Highmore is one of the earliest of modern authors, if not the earliest, to propound a reasoned theory of pangenesis. He now proceeds to mar this creditable piece of speculation, wrong though it be, by stating his belief that certain animals arise from the corruption of dirt, mud, and other animals, such as eels from mud, and flies, worms, and parasites from animal putrefactions. This, however, he ingeniously explains by assuming that the seminal particles belonging properly to a particular animal, may, in the corruption of a part or the whole of that animal, be reassembled to form a species of a different kind, such as a parasite, and he mentions as an example the mistletoe.

Highmore's account of the development of the chick is good, and it is otherwise interesting since it is the first piece of embryological research based on microscopical examination. The second is that of Malpighi. Highmore refutes the statement that the chick arises from the chalazae (Fabricius), and shows that the real source of the embryo is the cicatricula of the yolk—in this confirming Parisanus and agreeing (independently) with Harvey. He traces briefly the early development of the embryo and the spreading of the blastoderm. He saw the three vesicles of the brain in a four-day chick, and noted the flexure of the body. His description of the later stages is much more detailed. Sexual generation is explained by Highmore on the assumption that the seminal atoms of both parents are selected, mixed, and fall into their respective places under the direction of the

soul until the foetus is brought to perfection. The two sexes are necessary because the seminal atoms are of two kinds, which involves a difference in seeds and a separation of the seed bearers into sexes. These two kinds are (1) the spiritual or male seed which enlivens and activates the whole embryo, and (2) the material or female seed which nourishes, fixes, and cements the spiritual atoms together, so that they cohere to produce an organized whole. The resemblance to parents and determination of sex are effected by an internal struggle for dominance among the seminal atoms in every act of generation. At the time Highmore was writing it had not been demonstrated that the mammalian ovary, then known as the female testis, played a definite and important part in generation, nor had it been recognized that this organ was the homologue of the ovary of the egg-laying animals. We have seen, for example, that Harvey actually denied that the mammalian ovary had any concern in generation.

Wharton (1656) throws out a suggestion which bears directly on the question of the status of the mammalian ovary. He says that the female testes are intended to produce not only their own proper semen, but to receive a sufficient portion of the male semen, which, when mixed with its own, is then discharged, and takes up a position in the wall of the uterus where the foetus is formed from it. He also suggests that the male semen reaches the ovary by means of the uterus and Fallopian tubes. Everard (1661) appears to have been the first to experiment with the rabbit, which animal a few years later was the subject of de Graaf's classic researches, but he was not able to locate a foetus in the uterus until the eleventh day after coitus, when he found an embryo like a little worm having the beginnings of the red umbilical vessels. According to Descartes (1664) the embryo is the product of the confused mixture of the male and female semen, both of which are essential, which leaven and react on each other so as to produce the parts of the foetus. He points out, however, that lack of practical experience has prevented him so far from writing on generation, and he still has nothing to communicate on the nature and origin of the semen.

In 1667 Steno contributes a very important proposition. He states that the organs of female mammals, the so-called testes of the old anatomists, are not the same structures as the testes of the male, as Galen had supposed, but correspond with the ovaries of the egg-laying animals. Also they produce eggs, even in the viviparous dogfish, and are therefore as much ovaries as the egg-producing organs of the ovipara. He introduces the term *ovary* in this work. Thus Steno is the first to grasp the true nature of the mammalian ovary, i.e. that it is not a testicle, but he only states this as his unsupported opinion, and does not follow it up at the time. He is hence the first to suggest the identity of the generative process in the ovipara and vivipara, and he supports the doctrine that generation is by eggs. Later, in 1675, he publishes two papers on generation, which carry the work of this research much further, but in the meantime he had been anticipated by de Graaf in 1672, to whom we owe the discovery of the essential nature of the mammalian ovary. Kerckring (1671) also claims that there are 'ova' in the ovary of the vivipara no less than in the fowl. In the human female they have the size of a green pea, and one is extruded at each menstrual period. He agrees with Wharton that these eggs are fertilized by the male semen reaching the ovary by the Fallopian tube. The egg having been fertilized descends into the uterus, and in two or three days attains the size of a black cherry.

De Graaf published his great work on the female organs of generation in 1672. He dissected rabbits at varying intervals from half an hour onwards after coition, and partially succeeded in tracing the 'eggs', which he maintained existed already formed in the ovary, from the ovary down the Fallopian tube to the uterus—thus establishing the suggestion of Wharton. He found that the number of cicatrices or empty follicles in the ovary corresponded generally with the number of eggs in the uterus, and he was therefore able to demonstrate that the generative process was associated with changes occurring in the ovary, which is consequently essential to generation. Thus he discovered that the 'eggs'

of the mammal originated in the ovary and developed in the uterus—a conclusion which was not at first completely established, and obviously required for its confirmation very exact and skilful observation. De Graaf describes the 'ovarian vesicles', since named after him, or hydatid vesicles as they were in his time often called, which had already been seen by Vesalius and many other anatomists, and called 'ova' by van Horne in 1668. The latter name was given them because of their resemblance to the ovarian eggs of birds. De Graaf holds that ova are to be found in the ovaria or female testicles in all animals, such as mammals, birds, fish, and even in mules, whether oviparous or viviparous, though they vary in size in different species. They represent the essential principle in generation, and are not to be confused with hydatids. The ovary and eggs of birds are directly comparable with those of mammals. In mammals they undergo remarkable changes as the result of age and impregnation. After fecundation, which he believes must occur in the ovary, since the eggs cannot escape until they are fertilized, the ova are detached and conveyed to the uterus by the Fallopian tube, leaving the empty vesicle behind in the ovary. It must be emphasized that, although de Graaf recognized that the 'ovum' in the oviduct was much smaller than the ovarian follicles, he never saw the mammalian ovum—in fact he believed that the female generative substance only became *visibly* vesicular or egg-like after reaching the uterus at the end of the third day, and even then it must be sought for with great care. Nevertheless, he says, the primordium of the foetus in the ovary *must* be vesicular. In fifty-two hours after coition he suspects that the contents of the ovarian swellings [Graafian follicles] may have escaped, but he failed to detect any traces of them in the oviduct. In seventy-two hours, however, the swellings have ruptured and are quite empty,[1] and 'ova' are now found in the uterus and Fallopian tubes. Whilst it would not be correct to describe de Graaf as the first of the ovists, it was he, rather than

[1] Walton and Hammond (1928) state that the follicle ruptures generally about ten hours after coitus in the rabbit.

Harvey, who put that doctrine on a scientific footing, and was responsible for its general acceptance.

Le Grand (1672) supports pangenesis, which he says is confirmed by the inheritance of injuries and mutilations. The male and female semens meet in the uterus, and become entangled and worked up or digested by heat so as to form 'a rude delineation or rudiment of the animal from which afterwards all the parts are perfected and completed'. In 1677 C. Bartholinus, who was an ovist, confirms the existence of 'ova' in the ovary of mammals as described by de Graaf and Steno. The whole business of generation, he says, both in the ovipara and vivipara, turns on the production of eggs, which, however, can only produce a foetus when they are fecundated. It is certain that the only function of the male is to effect the fecundation of the ovum, everything else depending on the female alone. He agrees with Harvey, as against de Graaf, that the male semen enters the blood, and is not to be found in the uterus.

Leeuwenhoek (1683), in stating his views on the nature of fecundation, maintains that the eggs are impregnated by the seminal animalcula. It is necessary that one of the animalcula 'should get into a certain point of the yoak of the egg (which point is only fit to receive it, and give it the first nourishment, till such time as the egg comes to be sat on). But if no one animal should find this point, then the egg is unfruitful: and this may be a reason why there are so many thousand more animals in semine masculino than eggs in the female'. He judges that there may be ten thousand sperms to each egg. This passage has a remarkably modern ring, and it is surprising that Leeuwenhoek's surmise should have been so near the truth.[1] In answer to the criticism that if only one animalcule is sufficient to produce a foetus, why are there so many thousands in one drop of semen, he refers to the great wastage of seed in the vegetable kingdom. In 1685 Leeuwenhoek investigates the point whether the seminal fluid reaches the uterus. Harvey denied

[1] As Leeuwenhoek was not an ovist his views on fecundation are truer than he thought they were.

that it did,[1] and de Graaf believed that the male semen was only a volatile salt which affected the egg by contact. Leeuwenhoek now demonstrates the important discovery that living spermatozoa can actually be seen by the microscope in the uterus of the dog after coition. He concludes that the uterus and not the vagina is the part intended for the final reception of the male semen. He did not succeed in finding any eggs in the uterus after coition, although he frequently looked for them, but by eggs he understood the Graafian follicles, and was therefore looking for too large an object. Later, in 1722 and 1724, Leeuwenhoek's observations on generation are much less happy. He refers for example to the imaginary orifice of the Fallopian tube which is thought to suck the egg from the ovarium 'according to the old absurd notion'. His confusion of the Graafian follicle with the egg, which, however, was usual at the time, robs of any point his comparison of the size of the so-called egg with that of a foetus of the fifth day. Finally he scouts the idea of the animalcule passing through the Fallopian tube to the ovary to fertilize the egg *in situ*. Such statements, he says, require no further answer. He evidently has not heard of cases of ovarian pregnancy. Drelincourt (1685) is more correct. At certain times, he states, the ovaries are embraced by the funnels of the oviduct, which suck the eggs from the vesicles in which they are lodged. They then pass slowly to the uterus. In some unusual cases the male semen is forced as far as the funnels, where it encounters the eggs, and gives rise to conceptions in abnormal places. He compares the development of the egg in the uterus with the germination of a seed in the soil, the umbilical cord and its vascular connexion with the placenta being compared with the roots of the plant. It will be noted that Drelincourt mentions the ovarian vesicles [Graafian follicles] as containing the eggs—a suggestion of considerable importance, but so far only a suggestion. Lipstorp (1687) confirms Leeuwenhoek's views on the function of the seminal animalcula, and expresses

[1] Leeuwenhoek on more than one occasion disputes the accuracy of Harvey's statements on this question.

the opinion that only the male semen which contains the animalcula is capable of impregnating the ovum, but no evidence is produced for this impeccable statement. The difficulty that only one foetus is formed out of the vast number of sperms which enter the uterus is explained by Garden (1691) on the supposition that at only one point of the ovum can the sperm be received, and that point is the centre of the cicatricula or punctum or place of nourishment, which can hardly contain more than one animalcule.

The absence of experimental evidence is so conspicuous in the early literature of generation that what there is of it must be specially emphasized. Nuck (1691), who was an ovist, took a female dog on the third day after coitus, opened up the abdomen, and observed that two 'ova' were conspicuous in the left ovary. The left horn of the uterus was then ligatured about half way between the vagina and the ovary, and the abdomen closed. On the twentieth day after the ligature had been applied the animal was killed and examined, and in the left horn between the ligature and the ovary there were two foetuses, but in the lower part between the ligature and the vagina there was nothing. In the right horn there were three foetuses in the normal position. Nuck regards this experiment as proving that the two foetuses were the product of the two 'fecundated ova' in the ovary and not of the male semen, since there were no foetuses in that part of the uterus which had been cut off from the ovary. The experiment did not necessarily establish this point, but it was valuable as supporting de Graaf's views on the status of the ovary in mammalian generation.

Hartsoeker (1694) believes that each spermatic worm of a bird encloses a male or female bird of the same species, and, in coupling, a single worm enters an egg, where it is nourished and grows. Each egg has only one opening for the worm, and as soon as the latter has entered the egg the aperture closes, so that no more worms may pass. If by any chance two of them invade the same egg a double monster is produced. In mammals much the same thing happens, but the

worm becomes attached to the egg by its tail, and the egg acquires a connexion with the uterus. The tail of the worm becomes the umbilical cord, and the egg itself the placenta. Blood passes from the female parent to the egg and from the egg to the foetus, and back to the female again in the reverse order. Variations of this speculation, which professes to explain the formation of the placenta and umbilical cord, soon became very common. In 1708 Hartsoeker repeats it with slight modifications. He now says that the cicatricula of the fowl's egg is a small cell intended to lodge a seminal animalcule. There may be room for only one, or the opening closes after one has entered. The animalcule then develops into the foetus in the egg, to which it is attached by its tail, the latter structure including and finally becoming the stalk of the yolk sac. After observing that the spermatozoa are only active and vigorous in young men, but that in children they cannot be found, and in old men they are dead or languishing, a statement which occurs with variations and additions very commonly in the literature, Hartsoeker propounds an extraordinary panspermic theory of the origin of the male semen. The seminal liquor with its animalcula, he says, are separated out from the blood, which they reach via the gut or the respiratory organs, i.e. they are taken in originally with the food or respiratory air. In the body they develop, become perfect, and pass into the blood stream, from which they are transferred to the genital organs, where they are stored until wanted. Hartsoeker is silent regarding the history of the eggs. Fontenelle, in his Éloge of Hartsoeker, gives a version of this theory for which Hartsoeker himself is only partly responsible.[1] He puts it that invisible germs representing the primordia of the spermatic animalcula of all species, but not the ova, occur suspended everywhere in the atmosphere. They enter the body indiscriminately during respiration or with the food. Only those, however, which belong to the species of animal invaded reach the genital organ of the male, where they are nourished. This theory, or that part of it which he devised, Hartsoeker after-

[1] Pouchet repeats this story, but he doubtless took it from Fontenelle.

wards abandoned, admitting that it was bizarre and absurd.[1] The change of view was induced by a consideration of the facts of regeneration, which proved that if such germs were universal they could also be superfluous.

In his works published posthumously (1697) Malpighi describes having examined the ovaries of cows and other mammals. He sees Graafian follicles of all sizes up to that of a cherry, but does not believe that they ever leave the ovary. He finds something inside the follicle about the size of a millet seed, which he identifies as the unfecundated egg, and he thinks it is discharged spontaneously from the follicle. It could not always be found. The vesicles themselves are not the true ova, but serve as a protection for them. Malpighi fails to distinguish between a corpus luteum and an undischarged follicle, and in this respect he is less successful than de Graaf. The structure he discovered inside the vesicle cannot have been the mammalian ovum, but it may have been the ovum lying in the discus proligerus. Dionis (1698) is an ovist who applies the dictum *ex ovo omnia* to all animals and plants. He asserts, notwithstanding, that both parents are obviously necessary in generation, but admits that this view is not generally received. He favours a form of pangenesis as probably the soundest system of generation. Thus definite particles representing all parts of the body are *filtered off* from the blood, i. e. not concocted. These particles are surplus to nutrition, and are utilized to construct the foetus 'by ranging its various particles in due order'. Hence a new body is formed similar to the parent, but incomparably smaller. Dionis expounds, but does not accept, the beliefs of the '*Panspermatists*, who allege, that in the beginning of the world, God created all the eggs of animals and plants, and scattered them up and down the air, and upon the ground. They apprehend, that the eggs are taken in by the mouth, along with the aliment, or with the air we breathe in [cf. Hartsoeker]; and finding a passage through such pores as are qualified to receive them, are after-

[1] Leibnitz and Bonnet adopted theories of death and reincarnation which fall into the same category as Hartsoeker's.

wards fecundated by the male seed; so that when a woman swallows several eggs, it is only those which contain little men that are qualified to insinuate themselves into the ovarium, as having a size answerable to the mold of that part'. Views such as this were evidently responsible for the satire published by Hill in 1750.

The work of Launay (1698) contains no original observations, and even the speculations have only a humorous interest. For example, in discussing the spermatozoa, he urges that their number alone is a sufficient obstacle to their having any relation to generation.

'A large swarm must present themselves simultaneously to fertilize one egg. Of necessity there would be a battle, in which the most vigorous worm would have to destroy all the others. But after so fatiguing a contest he would not have sufficient strength to take possession of the cell in the cicatricula of the egg. And can one think otherwise? And will any one say that these worms arrive in such great hordes only to witness the victory of one of their number, who is respectfully permitted to enter the cicatricula at the expense of their own pretensions? No, and do not forget this, it is necessary that all the other worms which have been vanquished in the attack on the cicatricula should perish everlastingly, and their pitiless historians can hold out to them no other prospect.'

Andry (1700), though a convinced and thorough-going animalculist, does not agree that the egg has no concern in generation. Animals only become capable of generation, he says, when the spermatic animalcula appear in the testis in their fully-developed mobile form. Andry, it may be mentioned, forestalled the experiments which were employed by Pasteur and Tyndall to reveal the presence of floating or suspended particles, by passing the rays of the sun through some vinegar in a glass, when the passage of the rays through the liquid showed that it was full of animalcula. Andry believes that the function of the egg is to receive, enclose, and nourish the spermatic worm. The place where the egg breaks off from the ovarium, which, he says, following Fabricius, resembles that where the fruit breaks off from the stalk, is marked by a small opening, by which the spermatic

worm enters the egg. The reason why there are so many worms is that the chances of any one of them finding this opening are exceedingly remote. After leaving the ovary the egg passes into the uterus, where it is surrounded by the spermatic worms, of which it is incapable of receiving more than one. A friend of his, a physician, 'a man of extraordinary skill in physic', suggested that the opening of the egg was guarded by a valve, so that when a worm entered the egg the valve prevented it from coming out again. The worm also could hold the valve fast by its tail, and exclude any other worm which might attempt to enter. Andry remarks that this opinion 'seems very probable'. In his last edition, however, he does not go so far as this. He omits the reference to the learned friend, and also to the valve, and now says that more than one worm cannot enter the egg because the cavity of the egg is proportionate to the volume of the worm, and there is no room for a second. Nor is it possible for the worm which has entered to bend itself round and escape from the egg. This harmless and ingenuous speculation developed into the following fairy tale, which is generally attributed to the defenceless Andry: 'A spermatic worm seeks out the ovary, slips into an egg, closes the door behind him with his tail, and proceeds to develop. If several attempt to enter the egg at the same time they become enraged and strike each other, breaking and dislocating their limbs, and thus giving rise to monstrosities. Even at this stage the spermatozoa are endowed with the nature of the animals to which they will give rise, for those of the ram already live in flocks.' Buffon ignores this version and quotes Andry correctly, but Cuvier remarks that the theory has an air of pleasantry, and should be considered only as an idea thrown out by a man of imagination. It is repeated with variations by several contemporary authors, and in modern times by Burdach, Lewes, and Radl. It probably originated as a satire on the credulity of the animalculists.

In 1704 Geoffroy and Du Cerf combined several contemporary speculations into the following system: The spermatic worm is carried by the oviduct to the ovary. The

egg which is most ripe, and of which the cicatricula is the most open, receives the worm without difficulty. The little animalcule attaches itself by its tail to the membranes of the [Graafian] vesicle which it will enter. The tail is a strand composed of many small vessels, and it already corresponds with the umbilical cord of the foetus, by which nourishing juices are conveyed from the animalcule to the egg [follicle], and from the egg to the animalcule. Owing to this reciprocal connexion the animalcule and the egg constitute a single body. The whole, having undergone growth, escapes from the ovary and takes up its position in the uterus, the spermatic worm becoming the foetus and the egg the placenta.[1] The cicatricula of the egg normally admits only one spermatic worm, but if by any extraordinary chance it is large enough to admit more, many-headed monsters may be formed, and other members of the body may be multiplied according to the number of worms introduced. Méry (1704) opposes the ovist system, and points out that the Graafian follicles cannot be detached from the ovary and are therefore not eggs. They contain only a liquid which itself cannot represent an egg. He denies also de Graaf's contention that the number of cicatrices in the ovaries corresponds with the number of foetuses in the uterus. Hence some other explanation of the cicatrices must be provided. According to Bellefontaine (1712), the spermatic vermiculi are the real agents in generation and all animals are propagated by them. The eggs are fecundated *in situ* in the ovary. A new method of fertilization is suggested by Bradley (1721). The male animalcule is necessary to impregnate the egg, and it does so either by passing direct into it, or the egg is wounded by the animalcule, which then becomes enclosed in the scar in much the same way as a gall grows round an egg deposited in an incision made by the parent insect.

Vallisneri (1721), in spite of repeated searches, never succeeded in finding ova in the Graafian vesicles of the Vivipara, nor can he always confirm de Graaf in recognizing

[1] The translation of this passage may not convey the author's meaning correctly, owing to the ambiguity of the original.

an agreement between the number of empty vesicles and of foetuses in the uterus, although in the ewe this agreement obtained. He believes that when a vesicle is emptied it disappears, and another begins to develop as a provision for the next generation. The human ovum, he says, is not known, and his conjecture that it may be concealed in the corpus luteum is an indication of his lack of understanding of the ovarian cycle. He confirms a conclusion already in course of proof that the ovum of Vivipara is not identical with the Graafian vesicle, by finding in the Fallopian tube shortly after coition an 'ovum' which was much smaller than the vesicle from which it had burst. As, however, no author before von Baer had seen the mammalian ovum, it is not always certain what structures are defined by the terms ovarian vesicle and corpus luteum. Vallisneri holds that the eggs are fertilized in the ovary by the spirit of the male seed, which ascends the oviduct and awakens and kindles in the egg a kind of spasm. Maître-Jan (1722) accepts the common belief that fecundation occurs in the ovary, and that the tail of the seminal animalcule is a cord formed of many small vessels and becomes the umbilical cord of the foetus. An attempt to explain the 'marvellous and almost incredible phenomenon' of regeneration is made by Gesner (1737). The elements of the semen of all species, he says, are scattered universally over the surface of the earth [panspermy]. These elements are taken in with the food and distributed to all parts of the body, where they begin to develop, and hence become surplus to the needs of the organism. This may be righted by initiating fresh growths, but another outlet is found when a portion of the body is removed experimentally or destroyed naturally, the excess of nourishing juice and semen of this particular part being thus able to replace the lost or damaged tissue.

Boerhaave (1744) has very sound views on the course of events in Mammalian generation—the growth of the 'ovum', its escape from the ovary into the Fallopian tube leaving a scar on the ovary, the passage of the 'ovum' into the uterus, and its fertilization by a sperm sometimes before, but usually

after, it reaches the uterus. He is also alive to the significance of abnormal conceptions in the abdominal cavity, the ovary and the Fallopian tube, and he disputes Harvey's belief that the fecundating principle of the male semen is absorbed by the blood and conveyed by the circulation to the ovary. If this were so, he says, the ovum could not be fertilized after it had left the ovary, whereas fertilization after the egg has left the ovary is the normal state of affairs. Also on Harvey's theory superfoetations should commonly occur. Boerhaave subscribes to the then popular belief that fecundation consists in the entrance of the male animalcule into the ovum. He propounds a difficulty which he admits he is unable to resolve, but he throws out a suggestion which indicates the lines along which the structure of the placenta was afterwards explained. Since, he says, the ovum belongs to the mother and the foetus is derived from the father, whence comes the navel string, which includes both arteries and veins? If it belongs to the placenta, how can the arteries which originate in the embryo be explained, and if to the foetus, how are we to account for the veins which arise in the placenta? It seems as if one part of the navel string must be developed from the foetus, and another part from the placenta, the two conjoining to form the complete string. Boerhaave has not, of course, understood the facts, but the suggested interpretation is interesting and significant.

The well-known theory of pangenesis for which Maupertuis (1744) is responsible was itself derived from the Greeks, and in its turn was modified and developed by Buffon and Needham, Réaumur, and finally by Charles Darwin. The term Pangenesis was invented by Darwin (1868). Buffon differs from Maupertuis in one important respect only, viz. that his molecules are identical and not diverse. Maupertuis' theory is based on *elective attraction*, which in his time was a fashionable hypothesis, owing to its success in explaining alike the sublime motions of the heavenly bodies and the humbler phenomena of Chemistry. Hence there arose a universal gravitation, of which elective attraction was only one manifestation. According to Maupertuis, diverse mole-

cules from all parts of the body assemble in the genital organs, and there fall by mutual attraction, instinct, or memory into the corresponding positions which they occupied in the generating body. The result is a potential reproduction in miniature of the parental species. As proof that the molecules have specific affinities he cites the peculiarities of monsters. When a second head is present it is always attached to the neck, and when there are supernumerary digits they are always on the hands or feet. Extra toes never occur on the head, or an ear on a foot. He has also an explanation of hybrids such as the mule. In this case the molecules do not know how to arrange themselves. Since the parents belong to different species the affinities of the molecules are disturbed, and they are in doubt whether to arrange themselves as those of the horse or the ass, and in this uncertainty they are not arranged at all. Hence arises such defects as sterility. Maupertuis does not believe that eggs pass from the ovary down the Fallopian tubes to the uterus. The eggs which are alleged to occur in the uterus are only species of hydatids. In his later work of 1751 Maupertuis does not introduce any essential modifications into his system. He says that the elements necessary for the formation of the foetus float in the semen of the male and female parents, but the essence of each part preserves a kind of *memory* of its former status, in virtue of which it will always assume a corresponding role in the foetus. Thus the species is preserved, and the resemblance of young to their parents is explained. Excess or deficiency of these extracts or essences results in the production of monsters with superfluous or imperfect parts.

Harvey's assertion that fertilization is effected by a seminal aura or essence transmitted by the blood stream, and not by the material or grosser parts of the male semen such as the spermatozoa, is supported by Swedenborg (*c.* 1744), who denies that the spermatozoa ever reach the ovum. James (1745), like so many others, cannot reconcile himself to the wastage of spermatozoa involved in Leeuwenhoek's theory of fertilization.

'If', he says, 'three thousand million animalcules should be included in a quantity of male sperm sufficient for the production of one animal only, provided the animal is produced by one of these animalcules, all the rest are superfluous, and created for no end, but to be immediately destroyed: Besides, we must suppose, that Providence aims very ill, if obliged to load her engine so enormously, in order to be able to hit the mark proposed. But in all other instances we find, that the author of nature perpetually adopts much less compounded means in order to arrive at the destined ends. We have, therefore, great reason to believe that the generation of animals is not the only thing neglected, and accomplished in a manner extremely unartificial.'

This opinion is quoted in full because it voices a very common and a very natural criticism of fertilization by a single spermatozoon.

Procope Couteau (1748), notorious for his method of sexual birth control, believes that the male semen reaches the ovary, penetrates the egg, and mixes with the female semen, producing an efflorescence. The foetus is derived from the semen of both parents according to its relative abundance in the male and female at the time. The male has two testes of unequal size—one for producing males, and the other, females.

The commanding position which Buffon occupied in the biological world in the middle of the eighteenth century, which he owed rather to an eloquent and forceful personality than to the possession of great scientific merit, was nevertheless inadequate to ensure the acceptance of his elaborate system of pangenesis, which was universally applauded but politely shelved. There can be no doubt that this theory was inspired by that of Maupertuis, of which it is a development and extension, and that Needham also was freely consulted. Buffon himself had the utmost confidence and pride in it. He assumes that organic molecules surplus to nutrition are dispatched from all parts of the body, and assemble in the gonads to form the seminal fluid of male and female, which is thus an extract of the several parts of the parent. Its presence explains the great work of generation. These molecules are identical in nature and produce different

tissues in virtue of a diversity of arrangement, whereas the molecules of Maupertuis are diverse, and, therefore, in reassembling must each repair to its own station. Buffon believes that in most animals the molecules are incapable of reconstructing another individual without a mixture of the fluids of both sexes, in which the molecules of male and female unite, not at random, but according to affinities which were dispensed by the organs from which they arose. Sex is determined by the accidental predominance of male or female molecules in any particular combination. Male and female molecules are separately incapable of forming an embryo. Hence the spermatic animals, being aggregates of male molecules only, are incapable of union among themselves, or of expansion into organisms similar to those in which they are found. They are not little animals, but one of the basal and original constituents of living matter generally. They are active, non-corruptible, and neither animals nor plants, but occur in abundance in both. From this it follows that there must also be a female semen for transmitting the female organic molecules. The male organic molecules assemble in the male to form first of all the spermatic animals, and the female molecules in the Ovipara are lodged in the cicatricula of the egg, which latter forms a passive matrix and nourishment for them. In the Vivipara the uterus is the matrix, and eggs, being therefore superfluous, do not exist,[1] since the female semen is a fluid. In the sexless animals [e.g. Hydra] the organic molecules may produce new individuals in any part of the body indiscriminately. When the living organic molecules become superabundant they produce fortuitous aggregates, such as the tapeworms and thread worms which are found in the sealed cavities of the body. Paste and vinegar worms are formed in the same way, and have no parents similar to themselves. Buffon is consequently a heterogenist.

[1] He says elsewhere, however, that the eggs of the Ovipara are analogous with the 'glandular bodies in the testicles' [Graafian follicles] of the Vivipara, and that the cicatricula of the egg corresponds with the cavity of the follicles—both containing the female semen.

According to Buffon the foetus is built up by an Intrinsic, Synthetic, or Plastic Force, or Internal Mould. The male and female fluids mix, and therefore the activity of the organic molecules is inhibited, and they become fixed in positions corresponding to those which they formerly occupied in the body of the parents. Hence, for example, the molecules which were derived from the head of the parents will assemble in a similar order to constitute the head of the foetus. In this way a small organized body is built up entirely similar to the species from which the molecules originally proceeded.

Buffon differs energetically from de Graaf. There are no eggs in the testicles of the Vivipara, and what is seen in the uterus is not an egg, the absence of which in these animals has been demonstrated almost to a certainty. The systems deduced from de Graaf's work are absolutely chimerical—there are no eggs in the Graafian follicles, nor will any observer ever find them there. What the follicle contains is not a solid body or egg but a liquid, which is the true female semen holding the female organic molecules. When the follicle is ripe it acquires an opening, and its contents fall drop by drop into the horns of the uterus, where they encounter the male semen, and the foetus is produced out of the mixture of the living organic molecules of these two fluids. In the Ovipara a similar female liquid semen is present, but it is lodged in the cicatricula of the egg, which therefore must be compared with the Graafian follicle of the Vivipara. The contents of the cicatricula, the female liquid semen, combine *in situ* with the semen of the male to form the foetus, all other parts of the egg serving only the purpose of nourishing the foetus during development. These parts of the egg therefore correspond with the uterus of the Vivipara, and represent a species of portable uterus. There is thus a separate uterus for every foetus, whereas in the Vivipara there is only one. Buffon holds that the cicatricula of the fertilized egg in the Ovipara contains a little embryo in a state of suspended animation. The Ovipara must be interpreted in terms of the Vivipara, and

not in the reverse order. *Omnia ex ovo* is a false principle. It will be seen from this abstract that de Graaf attempts to find ova in the Vivipara, and Buffon to find female semen in the Ovipara. In the former case the egg is everything, but in the latter it is only a useful accessory.

Needham (1749–50), whose results were exploited by Buffon without adequate acknowledgement, considers that generation is not due to pre-existing germs. The generation of one body is brought about by the corruption of another, as the result of which active particles are set free for fresh combinations. All matter is in the last resort the same, and differs only in the state of refinement and mode of arrangement of its particles. Needham's system of generation is practically identical with Buffon's, and may be briefly summarized as follows: There exists in the body a seminal material, which infiltrates all parts of the organism like an *Internal Mould*. When it is in excess, particles representing every fraction of the tissues assemble in the semen, and provide the material for generation. In sexual generation the particles representative of the male parent combine with the corresponding particles of the female semen, and thus the foetus is formed by contributions from both parents. Sex is determined by the physical dominance of the particles of one or the other sex. The foetus so formed is not a specimen of the parent species in miniature, but its parts develop successively. Thus the resemblance of the young to *both* parents is explained.

The case for pangenesis is also taken up by Réaumur (1749), who puts it in his own inimitable way, but with little that is new.

'The great Descartes', he says, 'did not presume so much upon the strength of his genius when he attempted to explain the formation of the Universe as he did when he sought to reveal the generation of man. . . . For a mechanism presides over the composition of the smallest animal far different from that which controls those luminous and opaque globes, which astonish us by the stupendous grandeur of their mass, but which nevertheless exhibit only a small number of regular movements of which we have to seek the causes. . . . Let us

give free play to our imagination—even more than is permissible, and endeavour to discover the cause which produces an animal out of one liquor or the combination of two. Let us suppose that extracts from all the organs of the body have been conveyed to the ovarium—how prepared and conveyed need not detain us. Having arrived there, we must presume that they would be in a confused state—materials for making the eyes would be mingled with those belonging to the stomach, and so on. What agent is to disentangle this chaos, and to sort out into groups the parts which belong to each other? Everything, even philosophy, has its fashions, and in physics we are at the moment impressed with the splendour of that occult principle which passes under the name of attraction [gravitation]. Why should this principle be confined to the physical world, and why should we not employ it to explain *all* the phenomena of Nature? Let us suppose that it is this force which assembles by mutual attraction the materials which enter into the prolific liquors. We are now beginning to explain the miracle of the formation of the foetus. The chaos is indeed clearing, and unorganized collections of analogous particles have been formed, but how are these collections to be resolved into their individual elements such as vessels, nerves, and muscles? By what law of attraction can certain particles of the osseous mass be assembled to form the stapes, and how are the different organs assigned to their proper stations? To produce an edifice so complex it is not sufficient to multiply and vary the laws of attraction—it is necessary to endow that attraction with the most perfect understanding.'

Réaumur mentions an author who had sent to the Academy a paper in competition for a prize on the *Nature of Motion*. According to this work an animal is nothing but an assemblage of a multitude of animalcula of indefinite smallness. Sensation is explained on the assumption that chains of these small creatures, hooked together by their paws, extend from the external parts of the body to the seat of the soul in the brain. A stimulus is thus conveyed to the brain by being passed along the chain, the terminal member of which communicates it to the soul. Réaumur adds that this work is still in manuscript form. 'The architect who presides over the construction of the living edifice', he says, 'must know as much as the architect who produced the universe. We cannot, therefore, hope to explain the first formation of an

animal.'[1] Nevertheless it must by no means be concluded that we cannot reasonably expect to reach a greater knowlege of the generation of animals than we have already. Réaumur is confident that breeding experiments and a study of hybrids will give us much greater insight into this curious problem than the microscopical observations of Leeuwenhoek and Hartsoeker, and he proceeds to indicate in detail a series of experiments which would settle definitely the part played by each parent in the production of the foetus.[2] For many years, he says, he has been breeding fowls to this end, and is in a position to publish his final results. In his work of 1749, however, he gives no hint of the nature of his conclusions, but promises to incorporate them in a separate memoir. He leaves it at that, for the promised memoir was never published.

Astruc (1765) supports the system of eggs, and their development in the Vivipara, which was propounded by de Graaf, but his views on fertilization are somewhat divergent. In the conception of each foetus, he says, the female furnishes an egg and the male a vermiculus. The subtle parts of the male semen, but not the vermiculus, reach the ovary, and so affect it that the descent of the ovum follows. The ovum meets the vermiculi in the uterus, and one of them passes into the egg by a special aperture. The egg and the vermiculus together form the foetus and its membranes, the male and female being equally concerned, but the vermiculus provides the embryo itself, and the egg those accessory but still essential structures—the foetal membranes, by which the foetus derives its nourishment and effects its attachment to the wall of the uterus. He supports this view because it assigns parts to the two sexes, and makes use of both eggs and vermiculi in generation, but he admits that it is very vague on the essential nature of fecundation and how it is effected, nor does it

[1] Or: If we do not expect to comprehend the macrocosm, no more can we expect to understand the microcosm.

[2] Ramström (1759) asserts that the external form and physiological ego of the hybrid are derived mainly from the father, and the less superficial parts from the mother. It is evidently work of this type that Réaumur has in mind.

explain those extra-uterine pregnancies which undoubtedly occur.

The celebrated Harvey, says Haller in 1766, was the first who denied that the male semen reached the uterus, and he was emphatically right in this. After coition it is easy to find the male semen in the vagina, but only very rarely is any found in the uterus. Later, Haller is disposed to correct this assertion, having found the male semen in the uterus of the sheep. Haller denies that the ovarian vesicles of the Vivipara are eggs, but allows that the first rudiments of the animal are to be found in the ovary and in the Graafian vesicles. When the vesicle is ripe it forms a projection, which swells up, bursts and discharges its humour and some blood into the funnel of the oviduct, which embraces the ovary. All his own work, says Haller, proves that it is in the ovary, even in the Vivipara, that the body is found which, when fecundated during coitus, becomes an animal, the funnel of the oviduct receiving and passing it on to the uterus. Further, since well-marked and almost perfect foetuses may be found in the ovary, it is obvious that life must originate there. It is therefore certain that neither in the uterus nor in the funnel of the oviduct does conception occur. This is proved by the fact that a fowl, after one impregnation, produces many fertile eggs, but as they must pass down the oviduct in succession, most of them must have been in the ovary at the time of fecundation. In the sheep during the first seventeen days after coition, and in spite of repeated careful examinations with a lens, Haller was unable to find any trace of a foetus, or indeed of any definite body, in which experience he agrees with Harvey and Sylvius. Voltaire (1777) admits that Buffon's theory of organic molecules is very attractive, exhibiting as it does much sagacity and imagination, and yet it is not acceptable. His objections, however, do not exhibit a close acquaintance with Buffon's speculation, as may be gathered from his facetious remark that 'an organic molecule may become an Alexander or a drop of urine'.

The first observer to demonstrate the epoch-marking

experiment of artificial fecundation, using both the discharged semen and the expressed juice of the testis, is Spallanzani (1780).[1] Malpighi had previously made the attempt without success. Spallanzani points out, but not for the first time, that in the frog the fertilized egg, whether fecundated artificially or naturally, alone proceeds to develop, whereas the unfertilized egg decomposes—a conclusion which was later confirmed by Dumas and others. Spallanzani successfully practised artificial fecundation in various Amphibia, an insect, and the dog. His further experiment of thinning the male semen, and finding that a single drop of semen diluted with four, and even twenty-two, pounds of water is still capable of effecting fertilization, is of the greatest significance, since it discounts the importance of the male semen in the mass, and points to the spermatozoa as its essential constituent. It must not, however, be forgotten that Spallanzani maintained that semen deprived of its animalcula still possessed its fecundating properties. His evidence for this crucial assertion shows us Spallanzani at his worst. It rests on the following points: (1) The seminal liquor of two toads was found to be entirely destitute of spermatic worms, but was nevertheless just as prolific as 'that which most abounds with these diminutive animals'; (2) when the semen is mixed with human urine or vinegar 'the worms are all destroyed', but the seed does not lose its virtue; (3) when a few grains of seed are mixed with twelve, or even eighteen, ounces of water, the worms are 'so thinly dispersed through that large body of water' that not a single specimen can be distinguished, and yet it retains its fertilizing properties, as also does seed which has been kept so long that living worms cannot be found in it; (4) when a drop of semen is evaporated, the worms collect in the centre of the drop, but the peripheral zone, which is quite free from worms, is still prolific. 'These facts prove, then, irrefragably that the system of Leeuwenhoek and his followers is false.' Spallan-

[1] According to Spallanzani himself a preliminary account of his work on artificial fecundation was drawn up in 1779, but this paper is unobtainable in England, and it is not even certain that it was published.

zani was a skilful experimenter and an acute reasoner, but none the less he failed to realize that in not one of his cases does the technique absolutely exclude the occurrence of living spermatozoa. His conclusion that the male semen has no nutritive functions, and effects fecundation by acting simply as a stimulant on the heart of the preformed foetus, is a deplorable termination to a brilliant series of experiments, and an instructive commentary on his own reflection that 'the astonishment which we experience often prevents us from observing as we should the object which has aroused it'.

Spallanzani was also the first to separate the solid from the liquid parts of the male semen and to test each by itself. If, he says, spermatized water be filtered through cotton materials, it loses much of its fecundating power, and it loses it entirely if it be filtered through several thicknesses of blotting paper. Filtration through two papers produces a partially sterile filtrate, and the sterilization becomes more complete the more papers are used, until a filtrate which has passed through six or seven papers is absolutely sterile. If now the filter paper itself be expressed into water which contains non-fecundated eggs they at once proceed to develop. It is unfortunate that these important experiments did not come earlier in the investigation, for by the time Spallanzani had made them his mind was already averse from accepting the spermatozoa as the essential factor in fertilization. He realizes that the substance in which the fecundating virtue resides is left behind on the filter paper, but he failed to identify that substance with the spermatozoa. In 1825 Spallanzani's filtration experiments were repeated and confirmed by Dumas, who, however, concluded from them that the spermatozoa represented the vital constituent of the male semen. A similar conclusion, based on filtration experiments, was reached by Newport in 1851, but was not regarded as demonstrated.

Erasmus Darwin (1794) objects to Buffon's theory of organic particles on the ground that, as each parent assembles a complete set representing all parts of the body, 'there is no reason why the mother should not produce a female

embryon without the assistance of the male, and realize the *lucina sine concubitu*.' We have seen that Buffon is at pains to meet this point, and if his refutation is chimerical it is none the worse for that. The difficulty that if the embryo is derived from the male it cannot resemble *both* parents is dimissed by Darwin in the following passage:

'If the embryon be received into a fluid, whose stimulus is different in some degree from the natural, as in the production of mule-animals, the new irritabilities or sensibilities acquired by the increasing or growing organized parts may differ, and thence produce parts not similar to the father, but of a kind belonging in part to the mother.'

The original rudiment is derived entirely from the father, but, being only a living filament and not an homunculus, it is susceptible to modification during growth. All animals have a similar origin from a single living filament, and different forms and qualities have arisen as the result of the effect of the environment during the growth of the filament.

Some welcome experiments along the lines laid down by de Graaf were published by Cruikshank in 1797. He discredits animalculism, and even goes so far as to express disbelief in Leeuwenhoek's spermatozoa, but he does not discuss the Preformation Doctrine. According to Prévost and Dumas, Cruikshank was the first to see the early Mammalian ovum [i.e. early foetus] after de Graaf, and Cruikshank himself says that 'de Graaf had the fate of Cassandra, to be disbelieved even when she spoke the truth'. Cruikshank, who was an ovist, and believed that the ovum was really formed in the ovary, describes the calyces or cups in the ovary which secrete the ova. The cups themselves are extremely vascular, but the ova are transparent and have no visible blood-vessels. The calyces, after expulsion of the ova, enlarge and become yellow, and form the corpora lutea. Cruikshank confirms de Graaf, and finds ova in the Fallopian tubes of the rabbit on the third day after impregnation. He holds with de Graaf that conception occurs in the ovary, and the ovum escapes by rupture from the ovary, taking four days to traverse the Fallopian tube before it reaches its final position in the uterus. He claims to have recognized the foetus as such in the uterus

on the eighth day, whereas de Graaf could not find it before the tenth.

The prevalent opinion that the ova were fertilized *in situ* in the ovary was challenged by Prévost and Dumas. In 1824 these authors give an excellent account of the development of the Graafian follicles of the dog and rabbit, the formation of the corpora lutea, and the early development of the ovum. They soon begin to doubt, as others had done before them, whether the Graafian follicle is the egg, since no trace of it can be found outside the ovary. Also they are greatly struck with the smallness of the early developing ovum in the uterus compared with the vesicles of the ovary. Even the uterine ovum twelve days after coition is still smaller than the ovarian vesicle, although the developing embryo in it can be recognized without the least difficulty. They describe the rupturing of the surface of the ovary in order to liberate the contained 'eggs'. The split heals, the cavity that is left is obliterated, and the result is the formation of the corpus luteum. They did not definitely settle the nature of the body which emerged from the ruptured ovarian vesicle. The 'ovules' in the uterus are very small, being only one or two millimetres in diameter, whilst the vesicles are seven to eight millimetres at least. Hence it is necessary to distinguish between the vesicles or 'eggs' in the ovary, and the small 'ovules' found in the horns of the uterus, the ovules 'very probably' having been originally lodged in the interior of the ovarian vesicles. They found on opening very advanced vesicles that they contained a small spherical body *one millimetre in diameter*, but the transparency of this body was much less than that of the ovules which were found in the uterus. They, therefore, do not claim that they have established the identity of the two structures, and recommend further research on this point. It is very doubtful whether these capable authors were the first to discover the mammalian ovum. De Graaf had known the early uterine 'ovum', but had not established its relations with the ovarian vesicles or Graafian follicles, although he was familiar with the difference in size. The dimensions

given by Prévost and Dumas must be held to rule out the possibility of their having seen the true mammalian ovum, either in the ovary or undeveloped in the uterus, but they probably saw the ovum in the discus proligerus. In the rabbit the ovum is only 0·12 mm. in diameter, and is just visible as a speck to the unassisted eye. On the evidence of this paper, therefore, it must still be accepted that we owe the first undoubted demonstration of the mammalian ovum to von Baer in 1827.

Whilst Prévost and Dumas were publishing their results, an article by Rolando appeared in 1823, which partly anticipates their peculiar version of epigenesis. Rolando's work obtained much credit at the time, and he was regarded as one of those savants who by their experiments had exposed the 'brilliant errors of Buffon, Bonnet, Spallanzani, and Leeuwenhoek'. He studied the development of each organ of the chick *separately*. The foetus, he says, is formed by the ovum of the female parent except the nervous system, which is derived from the male. The rudiments of the vascular system exist *before* fecundation, but it is only *after* fecundation that the nervous system appears. All the other organs are only appendages of these two systems, and are formed from materials brought to the appropriate places by the blood stream. The cicatricula of the *non-fecundated* egg consists of (1) a very small vesicle which becomes the amnion and the integument of the foetus; (2) a spongy disk which is the rudiment of the vascular system; (3) a small white body, the sacculus vitellarius of Haller, which gives rise to the alimentary canal. The *fecundated* egg shows in the centre of the cicatricula a small, scarcely perceptible streak only one twenty-fourth of an inch long, which is the rudiment of the nervous system. As this has been derived from the male parent, it must have been formed by the spermatozoon, but Rolando does not profess to have observed this. His system of generation is a combination of preformation and epigenesis, and is partly supported by Dumas (1825), who agrees that the male provides the nervous system and the female the vascular system—in fact he regards

this conclusion as a demonstrated truth. In 1827 Dumas returns to, and repeats, his conviction that fecundation is impossible in the ovary, but that it may take place either in the oviduct or uterus. In birds, fertilization occurs in the oviduct, after the yellow has been surrounded by the white, but before the shell is added. Spermatozoa never reach the ovary in birds, and are absent from the anterior region of the oviduct. In fertilization the male provides a spermatic animalculum and the female an ovum. It is assumed that the sperm penetrates bodily into the ovum through its envelope, and grafts itself on to the germinal disk, where it forms first the primitive streak of the modern embryologist and later the rudiment of the nervous system. In the frog Prévost and Dumas claim to have seen the spermatozoon within the gelatinous envelope of the egg. Dumas quotes from a communication received from his collaborator Prévost to the effect that *only one spermatozoon is required for each foetus*, and therefore the action of the sperms, which constitute the male agents in generation, is individual and not collective. Bory de Saint-Vincent (1827–30) vigorously denies the conclusion of Prévost and Dumas that only one fertilizing spermatozoon enters the egg and by doing so forms the nervous system of the foetus, on the ground that he cannot reconcile himself to the inevitable destruction of countless millions of zoosperms. The idea, he says, appears to him to be shocking, and it is one for which no sound proofs have ever been produced. He, however, confirms the statement that if ova are put into water they decompose, but if the water is mixed with male semen the eggs develop and produce foetuses. Also, filtered semen has no fertilizing action, but the residue has. He adds that if the male semen is distilled at a low temperature the vapour is inert and has no fecundating powers, but the residue is active, and has all the properties of the sperm. Dugès (1839) also attacks the speculations of Prévost and Dumas that the male first provides the nervous system of the foetus and the female then lays down the circulatory and digestive systems, drawing attention to the stupendous difference between the size of

the spermatic animalcule and the first rudiment of the nervous system.

The belated discovery by von Baer (1827) of the true ovum of Mammals, which, however, he called the ovulum, is not only important in itself, but still more so on account of its bearing on the history of embryology in general. It was the final demonstration of the truth of the Harveian dictum *ex ovo omnia*, and it established the egg as the morphological unit which lies at the root of the development of *all* animals, whether Ovipara or Vivipara. It is only another example of the profound but unfortunate truth that the human mind is eager to speculate but slow to observe, that when the discovery was made it was incomplete. Many embryologists had sought the ovum in the Graafian follicle, and some of them had thought they had found it. Von Baer found it concealed in the discus proligerus, as he called it, and he noted the relation of the ovum and discus to the parent follicle. But he missed the nucleus, an oversight which was perhaps natural at a time when histological technique had not been developed, and he compared the *whole* ovum with the nucleus of the unfertilized ovum of the bird discovered by Purkinje in 1825. The ovum was still unknown *as a cell*.[1]

The papers on the zoosperms published in 1840–1 by Lallemand are more fruitful in suggestion than in observation. He believes that egg and sperm play an equal and reciprocal part in the act of fecundation, and each contributes to it an organized living matter. The question of the function of the spermatozoa, he says, is intimately bound up with their origin, and the fact that they arise, like the eggs, from the substance of the generative gland is full of significance. Lallemand argues for the *fusion* of the egg and sperm, but not for the penetration of the egg by the sperm. The latter is grafted on to the surface of the egg, and forms the

[1] Schwann in 1838 expressed the belief that the ovum was a cell, but he did not consider that such an interpretation had been demonstrated, since the question of the identity of the vesicle of Purkinje with the nucleus was still in doubt. His own opinion was that the vesicle was the nucleus and the yolk the cell body.

first rudiments of the cerebro-spinal system and the external or active parts. The egg is responsible for the passive organs, i.e. the digestive and other internal parts. 'Generation is the detachment of a living part which may either develop separately, or obtain from another part the elements necessary for the subsequent production of a being true to type. . . . Generation is to the species what nutrition is to the individual.'

In remarking on the various forces which are supposed to operate in the production of the foetus, such as the *Nisus Formativus* of Blumenbach and the *Vis Essentialis* of Wolff, Allen Thomson (1839) remarks: 'As the knowledge of minute anatomy and physiology has increased, and the accurate observation of the process of development has been more extended, the number of such hypotheses has gradually diminished.' And on the nature of the process of fecundation he says: 'Neither experiment nor observation enables us to form the most distant conjecture what the nature of that action may be, which, from the influence of the male product, confers upon the ovum a new and independent life.' When these words were written, however, the solution of one important aspect of the problem of fertilization was already in sight. In the third series of his *Researches in Embryology*, published in 1840, Martin Barry reverts to the suggestion that the spermatozoon passes into the substance of the egg. He infers 'that the fecundating element of the seminal fluid penetrates, not only into the ovary, and into the interior of the ovum, but into the germinal vesicle, and even into a certain part of the altered germinal spot'. He adds that in many instances he has observed an attenuation or orifice in the zona pellucida, the form of the orifice 'suggesting the idea of the membrane having become cleft. . . . On one occasion, in an ovum of five and a quarter hours [post coitum], I saw in the orifice of the membrane [zona], an object very much resembling a spermatozoon which had increased in size. Its large extremity was directed towards the interior of the ovum. . . . I am not prepared to say that this was certainly a spermatozoon, but it seems proper to record the observation'. The figure shows quite a large

orifice in the zona pellucida, through which the supposed spermatozoon has presumably passed to become embedded in the peripheral cytoplasm of the ovum. Barry states, quite correctly, that the ovum in the rabbit leaves the ovary in most cases nine or ten hours after coitus. His ovum, therefore, was fertilized *when it was still in the ovary*,[1] and whilst this is not impossible, it does not make the statement any the easier to accept. The split in the zona is another doubtful feature. In later papers published in 1843, Barry described an ovum of the rabbit of twenty-four hours taken from the Fallopian tube which had divided into two blastomeres, and between the latter and the zona he figures nine spermatozoa, as many as twenty being counted in another case. He also *thought* he saw some of the spermatozoa *within*, as well as between, the blastomeres of the ovum. In this case he does not describe any orifice in the zona. Here the evidence produced only relates to the penetration of the spermatozoa through the zona, but *not into the substance of the ovum*. In another paper, published in 1847, Barry states that the 'ovum becomes fecundated by the introduction of a substance from the seminal fluid into the hyaline centre of the germinal spot'. It is obviously impossible to allow that Barry actually observed the fusion of the spermatozoon with the ovum, but we must admit that he demonstrated the first stage of the process, namely, the passage of the spermatozoon through the zona pellucida. He himself, however, always regarded the major discovery as his own, and his last hours were employed in drawing up a review of his microscopic observations, in which his claim to have revealed the nature of fertilization occupied a prominent place. Barry's results met with little favour. Important contemporary authorities such as Wagner and Leuckart, writing in 1849, expressed the following opinion:

'The truth is, "the *how*" of the fecundation is as far from our knowledge to-day as it was thousands of years ago; this process is still enveloped in what we feel inclined to consider "its sacred mystery".

[1] He clinches this point by stating that before the discharge of the ovum from the ovary the fissure in the zona pellucida 'very probably closes'.

It would be different if we could prove that the spermatozoa really yielded the material foundation for the body of the embryo; that they penetrated into the ovum, and were developed into the animal (which was the assumption of *Leuwenhoek*, *Andry*, *Gautier*), or else, that they become metamorphosed into the central parts of the nervous system. However, we are now convinced that all these assumptions are without any foundation. The import of the spermatozoa must be a very different one. But this is the very point of which we know nothing.'

They agree, however, with Kölliker 'that it is the spermatozoa which, by their contact, fructify the ovum'.

The second claimant to the discovery of the penetration of the spermatozoon into the egg is Nelson, whose preliminary and final papers were published by the Royal Society in 1851 and 1852. His material is the *Ascaris* of the cat, and he says that

'at the commencement of the oviduct the ovules become detached, separated from each other, and propelled singly along its interior. Here the gelatinous ovule meets the tubular spermatic particles, and is surrounded on all sides by them. They are at first seen to be merely applied against the ovule, but by degrees the margin of the latter presents a rupture, some of the vitelline granules are displaced, and the spermatic particles become embedded in the substance of the yolk itself. While the penetration of the spermatic particles is going on, a chorion, secreted by the oviduct, surrounds the ovule, forming a spherical envelope, within which the germinal vesicle, the granular yolk, and the imbedded spermatazoa, are enclosed. The spermatic particles after penetration are seen to swell, become transparent, and ultimately to dissolve. . . . I have seen the spermatic particles in all stages of penetration, from mere contact to perfect involvement within the ovule. . . . The present investigations appear to be the first in which the fact of the penetration of the spermatozoa into the ovum has been distinctly seen and clearly established, in one of the most highly organized of the Entozoa.'

Nelson figures the ruptured surface by which the spermatozoa enter the ovum, and shows as many as twelve of them embedded in the cytoplasm. Two points arise on this memoir—did Nelson see the spermatozoa at all, and if so did he trace their passage into the egg? To the first of these

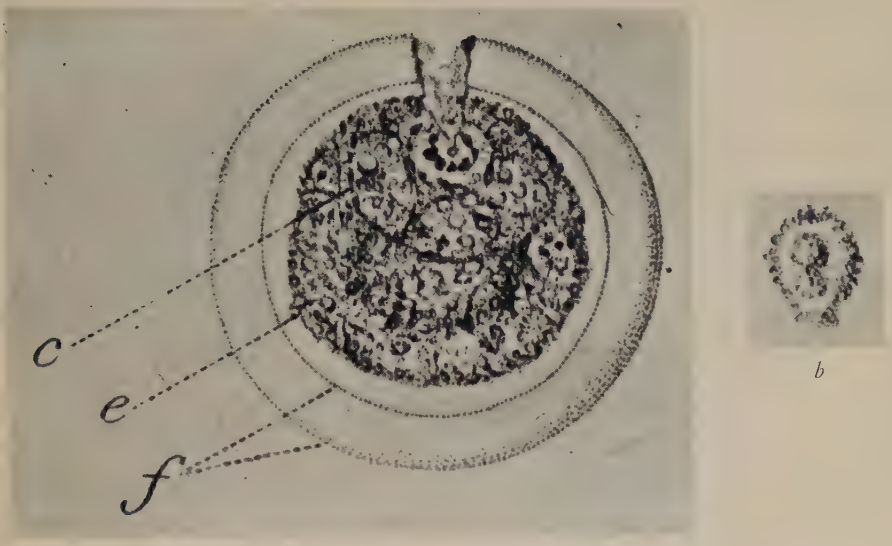

FIG. 20. Barry's 'fertilized' ovum of 5¾ hours. c, the nucleus with the 'spermatozoon' apparently embedded in it. In *b* the 'spermatozoon' is shown separately

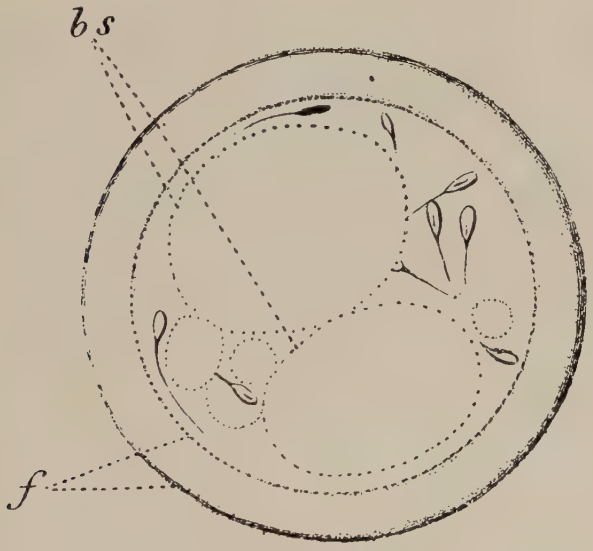

FIG. 21. Barry's ovum of 24 hours, showing two blastomeres and nine spermatozoa within the zona

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questions Bischoff (1853), who at first energetically opposed fertilization by penetration, but afterwards (1854) accepted and demonstrated it by his own observations, returns a very decided negative. He accuses Nelson of mistaking epithelial cells for spermatozoa, but subsequent research has made it clear that Nelson was successful in his identification of the peculiar spermatozoa of *Ascaris*. As regards the second point the verdict is unfavourable. The appearances which Nelson interpreted as enclosed spermatozoa have been proved to have another significance, nor is it necessary that the surface of the egg should rupture in order to admit the spermatozoon. Nelson, therefore, must be ruled out as a possible discoverer of the phenomenon of fertilization, and although he believed in the fact of penetration, his statement that many spermatozoa enter the egg, and afterwards disintegrate, shows that he had no knowledge of the actual events. It is interesting to note that Allen Thomson, who advised him, did not recognize in penetration a physiological process of any importance, but regarded it as purely mechanical and accidental.

In 1853 three memoirs were published which describe the entry of the spermatozoon into the egg. Keber maintains it in *Unio* and *Anodonta*, the spermatozoon being described as passing into the ovum through a rupture in its membranes. The evidence produced by Keber is of so flimsy a character, and his powers as an observer are so open to criticism, that we may proceed at once to a consideration of the views of the remaining two authors. Meissner worked at the Nematode *Mermis*. His description of the histogenesis of the ova, and the formation of a micropyle through which one or many zoosperms are admitted into the egg, where they are ultimately converted into fat globules, was refuted soon after it was published. The third author, Newport, presents us with a more plausible case, and he is usually credited with the honour of the discovery. His subject is the frog, and he opens by confirming the conclusion, stated many times previously, that the active agent in fertilization is the spermatozoon, and not the liquor seminis. This he establishes

by careful filtration experiments. At first (1851) he is strongly opposed to the idea of penetration. He says:

'Although we are as yet entirely without proof that any material influence or substance is actually transmitted from the spermatozoon on the surface of the ovum to the yolk in the interior, we have evidence that fluids are imbibed by the ovum by endosmosis through its tissues; and although not a trace of the spermatozoon is detected in the interior of the ovum, we have seen that it remains for a long time on the surface, and gradually disappears, apparently by diffluence.'

In his later paper, after stating that 'fecundation is not the simple result of the penetration into the egg of a *single isolated spermatozoon*, but probably of some definite number of these bodies, or of a definite amount of influence supplied through their encounter', he proceeds to give the following account of his discovery, dated April 18th, 1853:

'I have succeeded . . . in detecting spermatozoa *within the vitelline cavity in direct communication with, and penetrating into the yolk*. They were first seen by myself, in company with a friend, on the 25th of March of the present year (1853) within the clear chamber [entrance funnel] above the yolk, at about forty minutes after fecundation, when the chamber begins to be formed. . . . The presence of active spermatozoa *within the vitelline cavity* in the fecundated egg of the Frog may now be regarded as indisputable. . . . The spermatozoa do not reach the yolk of the Frog's egg *by any special orifice or canal* in the envelopes, but actually *pierce the substance of the envelopes at any part with which they may happen to come into contact*; as I have constantly observed while watching their entrance: some time after they have entered the yolk chamber they become disintegrated, and are resolved into elementary granules.'

Elsewhere, he refers to the 'penetration by the spermatozoa into at least the envelopes of the egg, and of the arrival at, and partial imbedment of these bodies in the vitellary membrane'. In his last paper on the subject, published posthumously in 1854, his previous results having in the meantime been confirmed by Bischoff, Newport describes the spermatozoa passing not only into the 'respiratory chamber' [entrance funnel] of the ovum, but also into the substance of the yolk. Again, however, the only evidence produced relates to the penetration of the *membranes* of the egg by

the spermatozoa so as to establish contact with the yolk, and having reached this point the spermatozoa are said to disintegrate. It may therefore be questioned whether Newport saw any more than Barry. The fact that he describes a number of spermatozoa entering the egg, and proceeding to disintegrate, makes it more than doubtful whether Newport ever observed the penetration of the spermatozoon into the *cytoplasm* of the egg.[1] We may, however, agree with Bischoff that in a general sense Newport 'is the discoverer of the phenomenon of the penetration of the spermatozoon into the egg by its own movement'. The assertion that fecundation is effected by 'one of the animalcula getting into the yolk of the egg' was originally made by Leeuwenhoek in 1683, and freely accepted since that time, but verification did not come until 170 years later.[2] The delay in confirmation can partly be ascribed to the undeveloped condition of microscopic technique. Newport used the half-inch object glass with the No. 2 eye-piece, and only occasionally the quarter-inch glass. His experimental equipment was of the simplest description. There is, however, no reason why Leeuwenhoek should not himself have demonstrated the truth of his own suggestion. The fact remains, therefore, that the early naturalists played a very minor part in the solution of the problem of fertilization, since the phenomenon of penetration by a *single* sperm, the fate of the sperm within the egg, and the equal participation of egg and sperm nuclei in fertilization were only completely demonstrated by the researches of O. Hertwig, Weismann, and Fol, between the years 1875 and 1879.

The segmentation or cleavage of the ovum was first observed by Swammerdam in the seventeenth century, but his description and figures were not published until 1738. He saw the first furrow of the frog's egg. 'The little animal', he says, 'was also divided throughout, as it were, into two

[1] Frog material is, of course, unsuitable, and Newport's microscope was inadequate, for this purpose.

[2] Leeuwenhoek's belief that only *one* spermatozoon enters the egg is logically required by his proposition that the spermatozoon represents the foetus, which robs the suggestion of that element of prescience which it would otherwise have displayed.

parts, by a very considerable furrow or fold. . . . On the opposite side of the foetus the furrow was not, by a great deal, so deep, so that it just looked like a superficial cut on the skin.' It is surprising that Swammerdam should have seen no more of the segmentation of the frog's egg, since his studies of that animal were both extensive and profound. He seems also to have confused the furrow with the medullary groove of the later embryo. Spallanzani (1780) describes and figures the first two furrows in the egg of the toad. When the eggs, he remarks, are 'examined with a glass of greater power, they seem to be marked with four furrows, which intersect each other at right angles, very like the fruit of a chestnut half opened—though the furrows are not bare, but covered with a very fine transparent membrane, which passes very tight round the rest of the egg'. These observations, however, probably because of their incompleteness and the lack of any discernible application, were neglected and forgotten, and it was not until 1824 that the classic description of the segmentation of the frog's egg by Prévost and Dumas focussed the attention of embryologists on this significant phenomenon. Other studies on cleavage quickly followed—in 1826 and 1834 on frogs and newts, 1835 a hydroid, 1837 starfish, nudibranchs, entozoa, and nematoda, 1838–9 the rabbit, 1839 a medusoid, 1841 aplysia, 1842 a fish, and 1847 a bird, but so far no one, except perhaps von Baer, had suspected that the segmentation of the egg was the key to epigenesis and the mechanism of generation. In the late forties and early fifties it was demonstrated that cleavage is a process of cell division initiated by the division of the nucleus of the ovum, which is the parent of all the nuclei of the body, and that the cells which constitute the embryo arise from the division of the segmentation spheres. Finally Newport, in 1854, laid the foundation of the new preformation by showing that the first cleavage plane of the frog's egg coincided with the median plane of the adult body. It was now possible to build up a system of descriptive embryology—a task which of necessity preceded any attempt to unmask by experimental methods the penetralia of the generative process.

VIII

RETROSPECT

THE present work is an attempt to record the complete history, as far as it is known to the writer, of a scientific adventure—the Preformation Doctrine. Other matters dealt with are supplementary and subordinate to this purpose. To justify the epithet 'complete' the historian must evaluate *all* the activities which were aroused and put in motion by the doctrine under consideration, and in particular he should not ignore the errors, repetitions, and vain philosophy which impede the progress of every scientific generalization. The path of science cannot be planned, but is ever tortuous and dendritic, breaking away into innumerable side-tracks, which terminate with monotonous and baffling regularity in the wilderness. When the purpose is at length attained, it seems incredible that so much time and energy should have been required and expended to achieve so modest a result. But however alarming such a review may be, it is unprofitable to neglect the causes which have combined to limit the expansion of scientific investigation in the past. The history of science can be written in such a way as to convey a wholly false impression, not only of the difficulties of research, but of the disastrous consequences which any failure to attack those difficulties by integrative methods invariably produces. For example, it would be literally correct to state that Küchenmeister was the first to establish experimentally (in 1853) the complete life cycle of a Cestode, but to go no further would be to take the difficulties and merit of that achievement for granted, and to ignore the element of time. If, however, the statement is amplified, and it is added that the discovery was the result of the efforts of six distinguished naturalists spread over a period of sixteen years, we begin to realize that the investigation must have been an exacting one, and we can only *completely* realize its perplexities, and appraise the genius of the time, by including in our survey the labours of that much larger company of

ineffective workers and critics, whose activities in the main served only to complicate and postpone the solution of the problem. A variety of causes appear to have operated to foster delay in early times. The absence of rapid means of communication to a large extent cut off an observer from the operations of his contemporaries. A modern scientific paper almost invariably begins with an outline of the problem to be attacked, and an account of the state of knowledge of that problem attained at the time. A display of ignorance of the literature, to say nothing of incapacity, is regarded as a lapse for which the author is severely criticized by his successors. Such ignorance in our own time is not only inexcusable, for sources of information are readily accessible, but wasteful in effort, since crude ideas and ill-informed discussion are thereby encouraged. Modern research is expected to be continuous and progressive. No one, however, can study the works of the older naturalists without realizing that their circumstances and standards were widely different. Their work was casual and sporadic, the production of isolated and often ill-trained observers, who were familiar with the writings of only the more picturesque of their contemporaries. Nor did they consider it necessary, or even helpful, to familiarize themselves with the work of their predecessors. The inevitable result was an unceasing flow of repetition and crude speculation, against which the genuine discoveries of a Malpighi or a Spallanzani stand out in startling and exaggerated relief. Hence it follows that the history of early science, provided it be fully and accurately represented, is a history of long periods of reiterative dullness, relieved frequently by the mendacity and unconscious humour of the charlatan, but only rarely by a work of genius. The complete picture, therefore, is a large canvas in which a few salient features serve only to condemn the poverty of the background, but to exclude the background from the picture would be to destroy at once its reality and significance as an historical document.

Another of these causes, and a most important one, 'lurking far down in the depths of human nature', is that fatal

preoccupation with philosophy which prefers the science of words to the austerities of serious research. If the history of Biology illuminates one conclusion before all others, it is that the most difficult task to which man has ever bent his mind is the simple and faithful observation of natural phenomena. Time and again we see how prolonged is an investigation which results in the establishment of but the simplest truth. And yet it is only by work of this type that any solid progress becomes possible. The wise injunction of Swammerdam—an injunction which, to his own confusion, he himself frequently neglected—that 'we must not surmise or invent, but *discover*, what Nature does' should be engraved on the lintel of every Biological Institution. It is expressive of the irony of the situation that we plume ourselves on that aspect of our work which is vain and argumentative, and condescend to the more modest but enduring labour of observation. It must be admitted that the older naturalists were grievous offenders in this respect. Of the eight massive volumes of the collected works of Bonnet nothing is remembered but his observations on the green fly and his experiments on regeneration. His tomes on the Philosophy of Nature, in which he exhibited such misdirected zeal, are opened only by the historian and the antiquary, whereas a more disciplined and sagacious development of his great powers might have made him the greatest naturalist of his time. His philosophical work was not only perverse in itself, but it presented a positive and obstinate obstruction to any real advance. Thus the state of development of the microscope was such that there was no reason why the Preformation Doctrine should have survived the seventeenth century, or that the main phenomena of fertilization should not have been discovered during the same period. This cause of failure in the older workers, due to philosophical diversions, is not always acknowledged in modern practice, but it is doubtless responsible for the prevalent and decided feeling that the biologist of to-day must be tied down to the inductive method, and leave the pleasures of the imagination to his vacant moments. Such an embargo

may be too rigidly applied, but at all events it reduces error, and never repeats the stagnation of the past.

The Preformation Doctrine cannot be justly estimated apart from its relations to contemporary thought. The belief in the mosaic cosmogony was universal at the time. Religious dogma assumed a mystical and precipitate origin of the world, and assigned to it a dramatic end. All life was created when the world was made, and must face extinction when the original impetus shall have been expended. Everything therefore was accounted for at the beginning, and nothing left for future creation. It was consequently the fate of a fluid and expanding science to be compelled to adapt itself to a rigid and inelastic dogma. To science was allotted the subordinate role of providing the material demonstration of the Divine Plan. The consequence of this may easily be predicted. Any principle which satisfied and expounded the Mosaic convention was acceptable, and the Preformation Doctrine, which allowed that there was no generation in Nature, but only the unfolding of a diminishing series of germs created at the beginning of the world, was adopted almost without question. Proof of it there was none. A few isolated observations of the most general and doubtful character were regarded as the unanswerable vindication of this accommodating doctrine. Thus when Swammerdam demonstrated the nature of the metamorphosis of insects, his results were interpreted as establishing preformation, and *if* they had applied to the earliest as well as to the final stages of development, such an interpretation would have been unassailable. When, therefore, microscopic examination revealed complexity of structure in early embryos, it was an easy and natural transition to the assertion that ultramicroscopic foetuses existed in the egg or sperm. For what could not be seen must not be dismissed as non-existent, and to complete the establishment of preformation it was only necessary to assume that the earlier stages were too small or transparent to come within the limits of microscopic vision. Even the missing evidence was not wholly wanting, and the gap was filled by the mendacity of some

and the mistaken credulity of others. Thus preformation not only satisfied the easy requirements of the seventeenth century biologist, but fell into its niche in the sublime scheme of the Creation.

The swamping effect of the Preformation Doctrine can only be fully realized when a review of the positive achievements of the early naturalists is attempted. During the seventeenth and eighteenth centuries important work was accomplished in the fields of comparative anatomy and physiology, and these successes stand as a significant commentary on the poverty of the results in generation. For over a century the most popular theory of generation involved a denial that such a process actually existed, or that it offered any scope for original research. Consequently speculation flourished unchecked in an atmosphere almost entirely free from the restraining influence of observation. It is true that microscopic work, indispensable in all early research in generation, presented great difficulties at that time. Leeuwenhoek, to his lasting honour, had shown how much could be achieved with a simple lens, and had 'made the conquest of a Universe peopled with invisible objects', but his skill both as an observer and lens-maker far surpassed that of his contemporaries and immediate successors. The old observers were obviously not proficient in the use of the microscope, which in most cases was available only to those who could make it for themselves. Even a hundred years later, Spallanzani was still preferring the simple to the compound microscope, and as recently as 1853 Newport was only *occasionally* employing, as his highest power, a quarter-inch glass. It took over a hundred and sixty years of research to establish that the spermatozoa were not homunculi, or parasites with a complex organization, but tissue elements of the animals in which they were found. The contributions of the early naturalists to the doctrine of generation may, therefore, be only too briefly summarized: (1) They discovered the spermatozoa; (2) they announced that the Vivipara, as well as the Ovipara, propagated by eggs, but this was not finally demonstrated until von Baer discovered the Mammalian

ovum in 1827; (3) although they had no conception of the nature of fertilization, they believed that a single spermatozoon entered the egg. This again was not demonstrated until modern times; (4) they propounded a theory of Epigenesis which was powerfully supported by Wolff in 1759, but only finally established by von Baer in 1828. That this meagre record is the direct consequence of the paralysing influence of the Preformation Doctrine is beyond question.

Even before the development of microscopic technique and the finer analysis of egg and sperm by experimental methods, the position taken up by the Preformationists was far from secure. When they called upon their opponents to admit the existence of ultra-microscopic beings and structures, they created a situation which transcended the confines of the inductive science of the time, and in which assertion was only limited by the elastic boundaries of possibility. Objections were met by postulating the presence of mystical qualities in the foetus, but this is to support an argument by contentions which would have great weight if only they could be established. It is impossible to study the history of biology without being deeply impressed by the failure of the biologist to face the implications of an attractive theory, and to base his judgement on *all* the aspects which that theory presents. Most scientific doctrines, even some modern ones, rest on certain fundamental *assumptions*, and on that sandy foundation a more or less imposing superstructure is erected. Admitting that useful and occasionally important results have been obtained by this method, the failures, which are more numerous, would have been short-lived and innocuous had they been scrutinized in all their bearings, and especially if the consequences which logically flow from them had been weighed in the balance. A speculation which makes a picturesque or academic appeal to the imagination, either in virtue of its ingenuity, or because it appears to throw some light on a long-debated problem, is assured of the warmest reception. The Preformation Doctrine is an excellent illustration of this point.

It enjoyed a life of well over a century. It is true that its life would have been curtailed but for the slow development of microscopic technique and the belated appearance of the Cell Theory. But even without these powerful weapons it could easily have been rejected on its merits. Take for example the statement which was commonly made, and is still made, that generation by preformation can be compared with a nest of boxes. Such a process is only possible on the assumption that each line of descent constitutes a strictly linear series, i.e. that each individual produces only one offspring; but as generation results essentially in an *expanding* series, it is a literal impossibility to proceed by way of a nest of boxes. Bonnet is one of the very few authors who have felt it necessary to consider this point, or to whom it occurred at all. Another corollary of encasement, which the preformationist wholly ignored, was the difficulty of explaining the inheritance of dimorphism, for example of male and female types of structure. Under the ovist system, when the series produces a male it finds itself in a blind alley, but the female can proceed to unmask future generations indefinitely, the converse being the case under the animalculist system. Hence the ovist must make special provision, other than by encasement, for the future production of males, and the animalculist of females. Since encasement in *both* sexes is precluded by the knowledge that an act of fecundation does not result normally in the production of two foetuses, it follows that unless every development into visible form is to stand a fifty per cent. chance of extinction, and therefore the elimination of one sex to be only a matter of time, the ovist must postulate two kinds of eggs and the animalculist two kinds of spermatozoa. In the former event there would be a male egg producing the non-encased male and a female egg for the encased female, whilst in the latter the female spermatozoon would produce the non-encased female and the male spermatozoon the encased male. On such an assumption the inheritance of sex by preformation becomes a speculative possibility. But how did the preformationists themselves deal with the sexual

problem? They did not deal with it at all—it was not even considered. Hartsoeker, in his earlier years, was almost the only preformationist who viewed with concern the difficulties which sexual questions presented to the preformation system of generation. In one sense no difficulty can exist, since every member of a species, male or female, was specifically created as such at the beginning of the world, and the only point to be explained is the *mechanism* by which each of them acquires visible form. It was, however, vital that the preformationists should be able to demonstrate that such mechanism, *so far as it could be observed*, was strictly consistent with the philosophical aspects of their doctrine. On this ground alone the old preformation should have been negatived, since, even in the seventeenth century, descriptive embryology was sufficiently advanced for the application of this test.

It may now be useful to summarize the various theories of generation prevalent in the seventeenth and eighteenth centuries. Rigid definitions of these theories, which are so related that they shade off into each other, are not easy to draft, and the difficulties are increased by the existence of certain avowed compromises, such as, for example, between preformation and epigenesis. Most early theories of generation, however, may be sorted out into two groups, corresponding more or less with preformation and epigenesis.

A. *Pangenesis.* This is probably the oldest theory of generation, and was resuscitated in modern times by Charles Darwin (1868), to whom the name is due. (The *whole* organism takes part in the generative act.) Pangenesis is a form of seminism in which, however, an attempt is made to trace the *origin* of the germ. Representative molecules from all parts of the body are assembled in the gonads, the semen therefore being composed of an essence of the entire parental body.) (In fertilization the male and female molecules are mingled, and fall into their proper stations and combinations in virtue of a directive agency, which was identified as an aspect of gravitation or elective attraction. The foetus therefore is constituted by equal contributions from *both*

parents. Pangenesis is related to preformation without encasement, and only differs from epigenesis in so far as it does not take the germ for granted, nor is it concerned with the precise stage at which a recognizable embryo can be distinguished. Cf. Highmore, Buffon, Réaumur.

B. *Precipitation.* The embryo is formed *suddenly* at the moment of fecundation, by precipitation from materials already assembled in the ovum. This theory has points of resemblance both with pangenesis and preformation without encasement, its distinctive feature being the instantaneous production of the foetus. It was first suggested by Harvey under the name of metamorphosis, but was developed in detail by Malpighi and Buffon.

C. *Seminism.* The generative principle resides in the male and female semen, the origin of these substances being ignored. An early system of seminism was propounded by Aristotle, who believed that the male semen represented the impulse or efficient cause, and the female semen was the substance on which it operated. This efficient cause is continually reappearing under a variety of names in the literature of generation, and in all cases it is an attempt to ascribe the formation of the foetus to a metaphysical agency, the nature and behaviour of which are beyond human knowledge. Thus we have the First Cause or Generative Principle of Harvey, the Vis Essentialis of Wolff, the Nisus Formativus of Blumenbach, the Vis Plastica of Buffon, the Mystical Host, Psychic or Ingenerate Heat, Anima Vegetativa, Vis Enthea, and the Vital Force of Modern Philosophy. Egg and sperm take no part in seminism, which, however, is only a modified form of epigenesis, as exemplified by Aristotle himself. A modern version of seminism was that devised by Maupertuis, who considered that the foetus was formed by the union of the male and female prolific liquors in the mass, i.e. *both* solid and fluid parts. But here again the embryo is not preformed, and must arise by epigenesis.

D. *Preformation*[1] (Vorbildung). Formerly known as *Evolu-*

[1] The term *Syngenesis* (Original Generation) is sometimes applied to the theories

tion or Pre-existence, but in recent times Whitman has distinguished between *Predetermination*, which is the new preformation—a physiological or potential preformation not capable of microscopic resolution, and *Predelineation*, which is the old morphological or visible preformation. (In the old preformation there is no true generation.) Nothing demonstrably new can happen in animal development. Preformation therefore makes no provision for variation, and stands for species fixed in structure, and limited in number to that originally created. The foetus already exists before fecundation as a complete miniature in either the egg or sperm, and generation therefore is nothing but a process of unfolding (Evolution) and growth without the addition of any new parts. Unorganized matter is incapable of producing an organized being, and since one part cannot function without the others, (the organism can only exist *as a whole*.) Hence it is necessary either to accept emboîtement, or to assume a *simultaneous* creation of all parts of the body in each case of development. Therefore fecundation has but a secondary importance in animal generation, and is concerned only with the awakening and emergence of the new individual, which is thus endowed with the 'vital commotion'. (There are various modifications of the Preformation Doctrine, most of which are concerned with the *extent* to which the foetus is preformed in the germ.) Preformationist theories in general accept the collaboration of egg and sperm in the formation of the foetus, and only differ in the view taken of the relative importance of these two factors.

Preformation is indissolubly linked up with *Emboîtement* or *Encasement*, (which assumes that at the beginning of the world the whole stock of each species, present or to come, was simultaneously created as an incalculable series, the members of which were enclosed one within the other like the concentric layers of a bulb. At each generative act the external member is unmasked, undergoes growth and

of emboîtement and panspermy. Lewes describes those theories of generation in which *both* parents are equally concerned as syngenetic. The *fact* of encasement has been referred to as Involution, and the *expansion* of the series as Evolution.

assumes visible form, the remaining members of the series repeating this process in succession from generation to generation until the series is exhausted. Encasement and organic evolution are consequently mutually exclusive. Preformation and emboîtement were formulated at the same time in the writings of Swammerdam and Malebranche, they are phases of the same doctrine, and it is impossible to separate them. Preformation without emboîtement is not only incomprehensible and explains nothing, but actually creates a situation which was so little contemplated at the time that few preformationists considered it necessary to discuss it. Preformation with emboîtement may be an erroneous and even a ridiculous doctrine, but it is none the less an intelligible and a coherent theory of generation. On the other hand preformation by itself involves, according to the point of view of our predecessors, an act of creation with each generation, and is hence on precisely the same impossible footing as epigenesis.

There are three aspects of the Preformation Doctrine, the first two of which have become notorious: (1) *Ovism.* The preformed foetus is in the ovum, and fertilization only supplies the vital impulse which results in its expansion. The term ovist or ovarist has been applied indifferently to the preformationist and epigenesist—in fact to any supporter of the doctrine of generation *ex ovo* as opposed to *ex animalculo.* It should, however, be confined to the preformationist to the exclusion of Harvey and his followers. Cf. Swammerdam, Malpighi, Haller, Spallanzani, and Bonnet. (2) *Animalculism, Spermatism, or Vermiculism.* The spermatozoon contains the preformed foetus, and the ovum supplies only a suitable place and nourishment for its development. 'Man engenders and the woman nourishes the fruit.' The wholesale wastage of spermatozoa in each act of fertilization was a fact which the older naturalists found it very difficult to understand and still more to believe. It was felt that if each spermatozoon were to be regarded as a *complete* animal then their destruction in such numbers was not only incredible but impious. The widespread support which animalculism

received[1] may be partly explained as the result of subconscious bias. Such a view endorsed the superior status of the male sex, through which alone the distinctive characters of a species were preserved and inherited. Cf. Leeuwenhoek. (3) *Compromises*. The embryo pre-exists *in an imperfect state* in the egg or sperm before fecundation, and is only *completed* by epigenesis. Or: the rudiments of the foetus consisting largely of the vascular system pre-exist fecundation in the egg. The nervous system only appears *after* fecundation, and therefore must have been introduced by the spermatozoon. Development is completed by epigenesis. Cf. Prévost and Dumas and Rolando.

E. *Epigenesis* (Nachbildung). (There is no original creation for *all* the members of a species.) Generation is effected *from time to time*, and each birth is a *new* formation, and the product or creation of the animal which engenders it. Epigenesis is compatible with variability, and no limit is placed on the future development of a species either as regards numbers or organization. It is therefore the antithesis of preformation and the fixity of species, (and the only primordial element in it is the desire and capacity for reproduction), which have been inherited from generation to generation since the beginning of the world. Until recent times epigenesis was essentially an *ex ovo* theory of generation, but it took the ovum for granted, and made no attempt to explain or trace its history,[2] and hence had no explanation to offer of the phenomena of heredity. (The question of the origin and continuity of the germ had no place in epigenesis,) although an explanation was offered by the preformationists. Cf. Harvey and Wolff.

F. *Panspermy*.[3] Often called dissemination or metamorphosis, but some authors distinguish between metamor-

[1] Cf. the parody by Bartholini (1680) of Job vii. 5: 'Vermiculi vivos nos torquent, et mortuos consumunt.'

[2] Harvey, however, ascribes the procreation of the ovum to a desire or appetite on the part of the uterus.

[3] The earliest use of this term in English which has been found is in the translation of Dionis dated 1703. The idea of panspermatism may be traced back to Anaxagoras, and the word itself to the Greek *Panspermia*.

phosis and panspermy. Generation depends on a primordial, indestructible, and unorganized substance or principle comparable with air, water, and the earth, but endowed with life. This diffuse organic matter was called into being at the creation, and was scattered abroad so as to populate the whole earth with germs, which invade the ovaries and testes of living organisms from time to time as opportunity offers. Its sum total has never been increased, and hence creative force has ceased to exist in Nature. At intervals and under suitable conditions the primordial living substance, whether free or enclosed, changes its status, and builds up a definite organism. Hence the term metamorphosis.[1] When an organism dies it undergoes disruption, and the generative particles return to their original state. Panspermy was invoked to explain the Animalcula Infusoria, which apparently sprang from nowhere, and owed their existence to no known means of generation. *Spontaneous generation* also can only be another aspect of Panspermatism accompanied by 'metamorphosis'.

The old problem of preformation versus epigenesis, laid to rest for a century by von Baer, has undergone an unexpected revival and metamorphosis in recent times. Epigenesis concerns itself only with the development of an externally visible or patent complexity, and it is now suggested that such complexity is but the manifestation of an invisible or latent mechanism beyond the reach of microscopic resolution. On this view the germ cell is not a simple unorganized unit, but a highly complex preformed microcosm, the architecture of which can in a measure be deduced from its reactions during development. According to some modern authorities the human mind cannot 'conceive how a self-determining system can increase its own initial complexity'. If this be admitted preformation must be a law of Nature, and epigenesis fundamentally impossible. There is

[1] Cf. Harvey's definition of metamorphosis: 'All parts are formed *simultaneously* out of material previously concocted, so that a perfect animal is born suddenly as in an insect emerging from a chrysalis.'

obviously much undoubted epigenesis not only in visible ontogeny, but even in the *behaviour* of the developing ovum, although the latter phenomena cannot be correlated with any structural peculiarities observable under the microscope. The old epigenesis, however, applies only to descriptive embryology, and at best is but a first step towards a comprehension of the final causes of animal development. Ontogeny may yet find its explantion in preformation rather than in epigenesis.

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